2011

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Recommended Citation

Pitts, Marie Louise, "The Influence of Golf Course Landscapes on the Occupancy and Reproductive Success of Eastern Bluebirds" (2011). *Dissertations, Theses, and Masters Projects.* Paper 1539626911.
https://dx.doi.org/doi:10.21220/s2-g8ke-e180

The Influence of Golf Course Landscapes on the Occupancy and Reproductive Success of Eastern Bluebirds

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A Thesis presented to the Graduate Faculty
of the College of William and Mary in Candidacy for the Degree of
Master of Science

Department of Biology

The College of William and Mary
January, 2011

APPROVAL PAGE

This Thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Science

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COMPLIANCE PAGE

Research approved by

Institutional Animal Care and Use Committee

Protocol number(s): IACUC-2008-01-02-5092-jpswad

Date(s) of approval: 2008-01-08 through 2011-01-08

ABSTRACT PAGE

With the increasing loss of natural landscapes to human developers, it is worthwhile to explore ways in which human-altered landscapes can also benefit native wildlife. Golf courses are relatively vegetated developed landscapes that may potentially double as usable wildlife habitat, especially for birds. Due to the remaining controversy over the value of golf courses as bird breeding habitat, there is a need for multi-scale studies that relate habitat to avian reproductive parameters. The eastern bluebird is a native cavity-nesting songbird commonly present on golf courses thanks to man-made nest boxes. Our study asked whether nest box occupancy and reproductive success varies with the proportion and arrangement of landcover on and around golf courses? We used field data from 288 nest boxes on nine golf sites in Southeast Virginia from 2007-2009. We conducted principal component analyses to create landcover variables and tested for correlations between landcover, occupancy, clutch size, hatching success, and fledging success at two box-centric and two site-centric spatial scales. We used a generalized linear model selection analysis for the local scale (25-m-radius around each box) and territory scale (100-m-radius around each box), and simple regression for the larger golf course scale (summation of all territories on a site) and landscape scale (1,500-m-radius around site centers). In summary, bluebirds were more likely to nest on golf courses that were surrounded by more agriculture and forest and less urban development, and in box territories that had more short grass with less mid-height vegetation. Bluebirds experienced higher reproductive success on golf courses that contained more fragmented patches of forest as opposed to open space. Within a golf course, higher reproductive success was observed in boxes that were locally surrounded by more grass and less forest.

To test the relationships observed in the correlational study, we conducted a field experiment in 2010 in which we relocated 60 nest boxes on three golf sites to new areas of the golf course. We collected field data and calculated landcover variables as before, then used simple regression to test our predictions at the local and territory scales. The correlational analyses predicted that bluebirds would nest more often on territories with more grass and less mid-height vegetation, but the experiment revealed no such relationships. However, the prediction that no relationships were present at the local scale held true with the experimental results. For reproductive success, the correlational analyses predicted that there were no relationships between landcover and reproductive success at the territory scale, but the experiment revealed increased reproductive success when boxes were moved to territories with more forest and less development. At the local scale, the experiment again confirmed our predictions by showing that boxes moved to local areas with more grass had increased reproductive success.

Though there were a few inconsistencies, there was evidence that landcover related to occupancy and reproductive success at multiple spatial scales, though the golf course scale is likely most important. This study provides research-based guidelines for golf courses to manage bluebird populations, and can serve as a case study for others attempting to understand habitat associations of cavity nesting species on other developed spaces.

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Acknowledgements

I would like to sincerely thank all of those who have given me academic (and personal) support throughout the development of this thesis. My advisor, Dr. John Swaddle, was the largest contributor to the conception, methodology, and interpretation of this project. He was also extremely supportive, patient, and available to discuss my progress and offer advise. Dr. Kerri Duerr, who was a post-doc at William and Mary during most of this project, was essential to my learning how to run the model selection analyses and making sense of the results. Dr. Daniel Cristol played a particularly important role in the design of the field experiment, and always gave me constructive advice. Allyson Jackson, another graduate student working on the Bluebird Project, was extremely helpful in familiarizing me with fieldwork protocols and teaching me to use ArcGIS. She also digitized a portion of the landcover that I used in my analyses. Dr. Swaddle, Dr. Duerr, Dr. Cristol, and Ms. Jackson, along with a team of past graduate and undergraduate members of the IBBS lab, all worked together over the years to collect bluebird field data from the golf courses in my study. Without them, this thesis would not have been possible. Dr. Paul Heideman and Dr. Matthias Leu were on my committee and were helpful in determining which direction to take the project. Dr. Leu was particularly helpful in helping me obtain the large-scale landcover data. Funding was provided by grants from Dr. Swaddle, as well as several research grants from The College of William and Mary, The Virginia Society of Ornithology, and The Williamsburg Bird Club. Thank you to my family, friends, and all the people who helped to keep me sane and keep things in perspective during the rough road of the graduate experience. Finally, I was honored to be able to complete this project in the presence of so many positive, skilled, and creative individuals.

Background: A Letter to Future Graduate Students

Williamsburg Bluebird Project

The concept for this study was born out of the long-term Williamsburg Bluebird Project, started by Dan Cristol and John Swaddle's labs (now the Institute for Integrative Bird Behavior Studies, or IIBBS) in 2003. The original goal was to examine the value of golf course habitats for eastern bluebirds (and sometimes other cavity-nesters), by comparing them to other habitats with similar structure and human disturbance (deemed "reference sites"). There are several resulting published papers available from these studies.

When I joined the graduate group in 2008, Allyson Jackson was still finishing her graduate work relating landcover to fledgling survival rates on golf courses versus reference sites. I was interested in contributing to the overall project, and her work with landcover and ArcGIS interested me. After talking with John, Dan, and Kerri Duerr (a post-doc at the time), I decided I wanted to explore the variation among golf course landscapes and how they related to bluebird occupancy and reproductive success.

If you are interested in adding to the project, there are still many unanswered questions that would be interesting to address. Following in Allyson's footsteps, you could use radio-telemetry to follow adult or fledgling survival rates. Ryan Burdge was a graduate student who looked at the effect of pesticide exposure on reproductive success, and there are still plenty of directions to take this work. No one has yet studied our bluebirds during the winter season, or you could use my methodology to look at landcover variation among the reference sites. Regardless of which questions you would like to answer, the Williamsburg Bluebird Project provides a nicely organized data long-term data set to utilize (and the fieldwork is pretty fun too).

Bluebird Databases

Thanks to the hard work of Dr. Kerri Duerr, data from all years of the bluebird projects are organized in a Microsoft Access database on the double-screen GIS computer in Millington 200. Before she joined IIBBS in 2008, graduate students had collected field data in their own way keeping their own versions of field data sheets with different coding styles and abbreviations for things. Needless to say, it was difficult to consolidate data. We did the best we could to bring all the data together in the same place and code everything in the same way. If you plan to contribute, PLEASE continue to add to the database in the same way. For analyses, R, SAS, and SPSS are available in the Millington 200 computers.

As far as my own project data goes, I have a folder on the GIS computer under: IIBBS drive – Williamsburg Bluebird Project – Marie. This should contain my landcover files, certain personal field data files, analysis, and results files. If you have questions, you can email me at: mariepitts@gmail.com.

Working with the Golf Courses

Something else you should be aware of is what it is like to work with the local golf courses. The golf course personnel vary in how easy they are to get along with, but as long as you are respectful of their wishes you shouldn't have too much trouble. You should start by contacting the course superintendant before the field season starts (often in February, so you can go out and clean out boxes before the birds start looking for territories). You should introduce yourself and your connection to William and Mary, briefly describe what your project is about, then ask when it is ok for you to borrow a golf cart to check the boxes during the week. Some courses want you to call every time you go out and arrive very early to avoid contact with golfers, others do not care when you show up. Course information sheets that include course contact information and specific notes will be in my file folder mentioned above. Overall, most of the sites have been working with us for some time and should be familiar with our involvement.

INTRODUCTION

As the human population increases, natural landscapes are converted into places for commercial activities, agriculture, residences, and recreation. To maintain biodiversity in the face of changing habitats, we need to identify the ways human-altered landscapes can benefit native wildlife. Golf courses are relatively "green" developed landscapes that may be usable wildlife habitat (Green and Marshall 1987; Terman 1997; Hodgkison et al. 2007; Colding and Folke 2009), especially for birds (Cristol and Rodewald 2005). In the United States alone there are approximately one million hectares of golf course land potentially available for avian populations (National Golf Foundation 2005; Cristol and Rodewald 2005).

Golf Courses are Conservation Controversies

It is controversial whether golf courses can provide quality habitat for wildlife. Though birds are present on golf courses (Colding and Folke 2009), some argue that golf courses are too fragmented, disturbed, and contaminated with pesticides to support healthy wildlife populations (Pearce 1892; Pleuramom 1992; Gange et al. 2003). Several studies have addressed how differences in golf course landscapes relate to avian diversity (Gordon et al. 2003; LeClerc and Cristol 2005; Merola-Zwartjes and DeLong 2005; Porter et al. 2005), but there is still a need for research that makes the connections between golf course habitats and avian demography (Colding and Folke 2009). Even if a golf course can attract birds, they may not necessarily be breeding successfully there. This phenomenon is referred to as an "ecological trap" (Dwernychuck and Boag 1972), where an area attracts organisms while negatively impacting their survival and reproduction. Without birth and survival rates, it is not possible to conclude that a habitat is beneficial for a species.

Conflicting Results for Reproductive Success on Golf Courses

The few studies that have measured avian reproductive rates on golf courses have provided conflicting results (Colding and Folke 2009). For example, Stanback and Seifert (2005) reported that bluebirds nesting on golf courses started laying one day later, produced slightly smaller clutches, waited 3.5 days longer to start a second brood, and produced nestlings in slightly poorer condition. In contrast, LeClerc et al. (2005) reported that bluebirds on golf courses produced 28% larger clutches and 17% more fledglings. Bluebirds also seem to exhibit maximized brood survivorship and nest box productivity when they encounter intermediate levels of human disturbance (Kight and Swaddle 2007). With the lack of demographic research and the contradictory findings in the literature, a deeper look into the relationship between habitat structure, occupancy patterns, and reproductive rates are necessary to properly evaluate golf courses as suitable wildlife habitat.

Landcover Matters

Most previous studies have grouped golf courses together into a single habitat type, which may not be the best way to evaluate golf courses given that they can vary substantially in their habitat structure both within their boundaries and in the surrounding landscape. Landcover, or the proportion and distribution of habitat types, is a factor that often affects avian nesting and breeding success (Breininger et al. 1995; Venier et al. 2004; Acevedo and Restrepo 2008). Golf courses can vary in proportion of different landcover types, such as forest, that are often important to birds. Varying amounts of forest can determine the availability of natural nesting sites, perches for foraging and territory defense, and cover from avian predators. Shrubs and other mid-height vegetation may also provide diverse plant and insect prey. Regularly mowed grasses may make ground foraging and predator detection easier, while developed areas such as buildings, roads, and cart paths, are often not as ecologically useful and may attract predators and competitors such as crows, cats, sparrows and cowbirds. As a whole, golf courses can provide more natural continuous cover, or contain fragmented areas of dense development (Terman 1997; Gordon 2004; Hodgkison et al. 2007). Even the landcover surrounding golf courses could affect the breeding success of birds on the golf course by altering the density of available nest sites in the area thus the competition level, or influencing predator and prey densities (LeClerc et al. 2005; Porter et al. 2005)

Spatial Scales

Given the value of studying landcover, it is also important to carefully choose the spatial scale(s) at which the study will be conducted. Whether examining mammals (Bowers and Dooley 1999), birds (LeClerc and Cristol 2005), or any other organism, there are a variety of ecological processes that interact with distribution and breeding success differently on smaller versus larger scales, and the scales should be biologically significant to the study organism. Exploring how population parameters are related to landcover on the scale of a breeding territory versus that of a larger landscape answer different but informative questions. For example, LeClerc and Cristol (2005) found that the proportion of forest cover both within the golf course boundary and within a 1.5-kilometer radius from the course center was the best predictor of a course's conservation value. On the other hand, some studies have found that it is not the landcover within a golf course, but around it that determines diversity (Laurance 2000; Porter et al. 2005; Turner 2005). Laurence (2000) discovered that even with a relatively naturalistic golf course, habitat features of the surrounding area can have a large impact on the wildlife within the course. Similarly, Porter et al. (2005) found that habitat variables on the golf course were relatively unimportant, but having natural landscape buffers surrounding the golf course resulted in higher bird diversity inside the course. Multi-scale analyses are valuable given that environmental features at different scales can affect organisms in different ways (Gutzwiller and Anderson 1987; Weins 1989; Thogmartin and Knutson 2007), and can be necessary to properly evaluate the value of a controversial habitat.

Study Species

With the continuing debate over the value golf courses as valuable bird breeding habitat, and the lack of research on how variation in golf course structure relates to demography (especially at multiple spatial scales), we conducted a study to address these questions for the Eastern Bluebird (*Sialia sialis*). Eastern Bluebirds are small thrushes (16-21 cm) native to most of the eastern United States. Males are easily distinguished by their blue upperparts, white belly and red-orange chest. Females are more dull-colored than males. Bluebirds are considered "partial migrants" because some members of some populations migrate south for the winter, while others stay year-round. They are secondary cavity-nesters, meaning they cannot make their own cavity but rely on those existing in rotting trees or made by other species. Bluebirds are considered "edge species" because they are attracted to forest/field interfaces. They prefer open habitat with sparse ground cover like mature pine woods and fire-maintained savannahs. They currently breed in habitats that include orchards, pastures, clear-cuts and burned tracts of forest, upland and swampy areas near developed areas, along rural railroad tracks and in park lands. During the breeding season (late March through September) bluebirds feed mostly on insect prey, while in the winter months they survive on small fruits. They are drop-foragers, perching on branches and visually searching open areas for insects within a 15-20 m distance, then dropping to the ground to eat the prey or carry it back to the nest (Gowaty and Plissner 1998).

Both male and female bluebirds help to defend a territory that averages 2.1 ha, though the territory size can be decreased by adding more nest boxes. As a semicolonial nester, bluebirds tend to nest in boxes closer to other bluebirds, A study in Maryland revealed bluebirds to prefer boxes near small shrubs, with short grass and nearby perches. There does not seem to be evidence of imprinting on nest site characteristics other than recognizing a cavity, and individuals have shown no preference for the presence or absence of predator guards on nest boxes. Nests are made entirely of pine needles, in which females tend to lay one egg per day. Clutch sizes range from three to six eggs (occasionally seven) with an average clutch size of five eggs. Generally, about 83% of eggs hatch, 75-90% of hatchlings fledge, and 55-84% of nests are successful. Two broods are usually laid per season, though three broods are not uncommon in the central part of their range (Gowaty and Plissner 1998).

Around 10% of nestlings die from starvation, exposure, or abandonment, and 2-10% have been shown to die from predation. Bluebirds are preyed upon by both ground predators (raccoons (*Procyon lotor*), chipmunks (*Tamias striatus*), flying squirrels (*Glaucomys volans*), black rat snakes (*Elaphe obsoleta obsoleta*)) and areal predators (House Sparrows (*Passer domesticus*), European Starlings (*Sturnus vulgaris*), Red-tailed Hawks (*Buteo jamaicensis*)) (Gowaty and Plissner 1998).

The species experienced a population decline throughout the nation in the mid-twentieth century, supposedly due to habitat loss and nest site competition with exotic invasive species such as the House Sparrow and European Starling. Thanks to the provisioning of artificial nest boxes across its habitat range, the population rebounded (Gowaty and Plissner 1998). Golf courses, with their abundant forest edges bordering fairways, were common sites for the placement of these boxes. Considering that bluebirds were present on our golf sites in numbers that would produce good sample sizes, that they nested in a range of habitat types, and that they used nest boxes that could be experimentally manipulated, they made a very appropriate study species for our research goals. The downside of this choice of study species is that results may not apply to less common species, particularly those that do not nest or forage on the open fairways characteristic of golf courses.

Research Goals

We wanted to answer the following question: Does variation in landcover both within and surrounding a golf course relate to variation in nest box occupancy and reproductive success? Using several local golf courses that already contained nest boxes used by bluebirds, we set up a correlational study that quantified landcover and related it to four responses: occupancy, clutch size, hatching success, and fledging success, over a three-year period. These relationships were studied at four spatial scales: two box-centric scales and two site-centric scales (where response variables were averaged for each site). A model selection approach was used for the box-centric scales to determine which landcover variables best explained variation in the response variables. Due to our low sample sizes at the site-centered scales, we used simple data plots to look for relationships. We then tested these results by conducting a field experiment the following year, where we relocated nest boxes to different areas of the golf course and used simple regression analyses to test whether change in landcover around a box led to the expected changes in the response variables.

Predictions

We predicted that several common golf course landcover types might be useful for bluebirds. Forest would likely be attractive to bluebirds as it provides natural nesting sites and perches for foraging. Mowed grasses could offer easy foraging sites for insects, and mid-height vegetation such as tall grasses and shrubs could potentially offer alternate prey and perches. Other landcover types may not be as useful to bluebirds, such as barren land like parking lots and buildings where human activity may drive the birds away. At a much larger scale, bluebirds may prefer more natural areas, but more developed areas such as golf courses, parks, or farmland may potentially be beneficial to reproductive success. Among all landcover categories, the amount of edge, or fragmentation, could play a role in these responses as more heterogeneous habitats may provide more edge for foraging opportunities. The public is increasingly interested in developing golf courses with attention to their role in an ecological context (McCarty 2001). Knowledge gained from this study can provide golf course managers and other interested parties with research-driven guidelines on how to maintain healthy bluebird populations.

Methods

Study Area

Our study area included nine golf sites within James City, York, and New Kent counties, in southeastern Virginia (Fig. 1). Golf sites were built 8 to 46 years ago in these locations, and nest boxes were present on all but one site at least three years prior to this study. All sites shared certain traits common to most golf courses: open areas with short, mowed grasses, sand traps, patches of tall grasses and shrubs, patches of tree cover, and impervious surfaces such as cart paths, roads, and buildings, though they varied in the proportion and arrangement of these land cover types. The landcover surrounding golf courses included varying patches of residential and business buildings, farmland, mature and regenerating forest, waterways and roadways. All golf sites regularly mowed fairways, but there was likely some variation in their degree of chemical usage (fertilizer, herbicides, and pesticides). However, this aspect was not addressed in this study.

As of 2009 there were a total of 288 nest boxes on these sites, with 98% of them placed within eight meters of the edge of fairways. Nest boxes were made of wood with 1.5-in. diameter openings. Most were attached to metal poles 1.5 m above the ground, though a few were directly attached to tree trunks. Most boxes also had predator guards in the form of cylindrical metal baffles around box poles, though the few boxes attached to trees had wire mesh protruding about five inches from the opening.

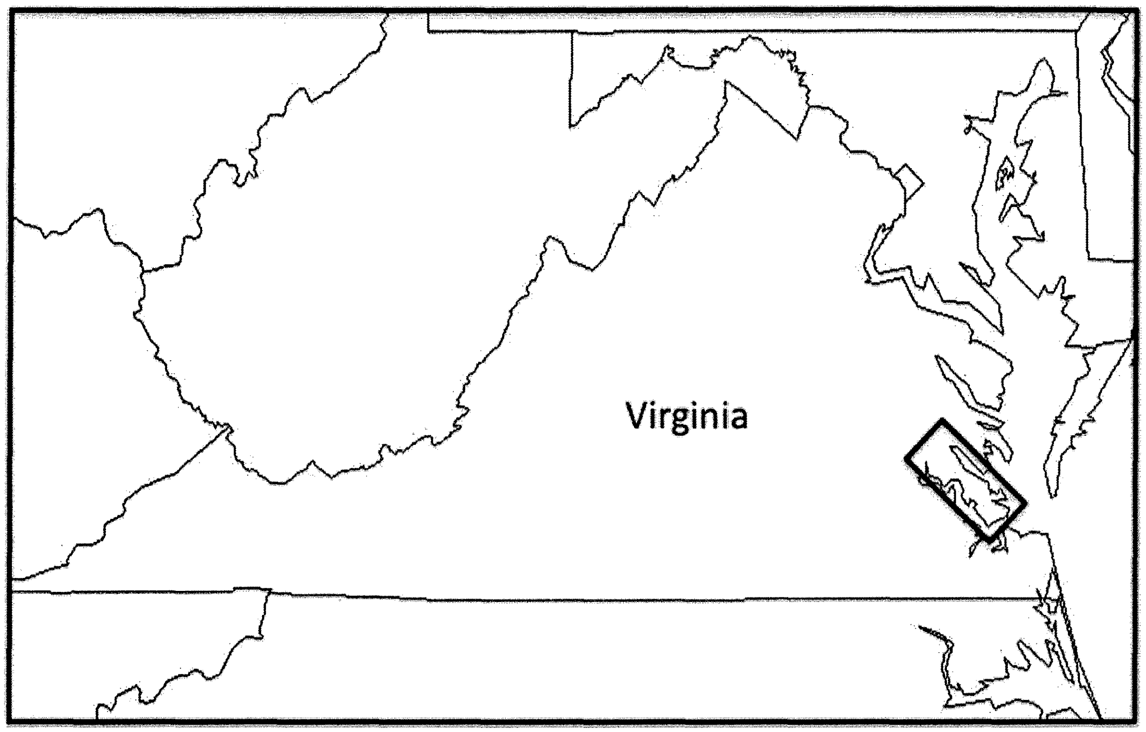

Figure 1. Study area in southeast Virginia.

Choosing Spatial Scales

We predicted that occupancy and reproductive success would vary with the proportion of landcover types and the amount of fragmentation (measured by the amount of edge) around nest boxes at four different spatial scales: local, territory, golf course, and landscape.

The local scale was defined as the area within a 25-m radius around each nest box (about 1,963 m^2, Fig. 2), and represented the landcover immediately around each box. Even at this small scale there was variation in tree cover, brush, and the amount of human traffic. Any of these features could potentially affect the likelihood of bluebirds nesting in one box over a neighboring box, or their reproductive success. This scale also encompassed the area within a bluebird's general visual range (15-20 m (Gowaty and

Plissner 1998)) and was potentially the habitat that the bird would evaluate as it determined whether or nest in a specific box (n = 605 nests).

The territory scale consisted of the area within a 100-m radius around each box (about 31,416 m^2, Fig. 2). This scale reflected the average eastern bluebird territory size of 21,124 m^2 (Gowaty and Plissner 1998), and represented the area in which parents were most likely foraging for food during the breeding season. Variation in landcover at this scale could affect the attractiveness of a potential territory, and variation in food quality and abundance at this scale, as well as chemical contaminants and human disturbances, could influence reproductive success (n = 605 nests).

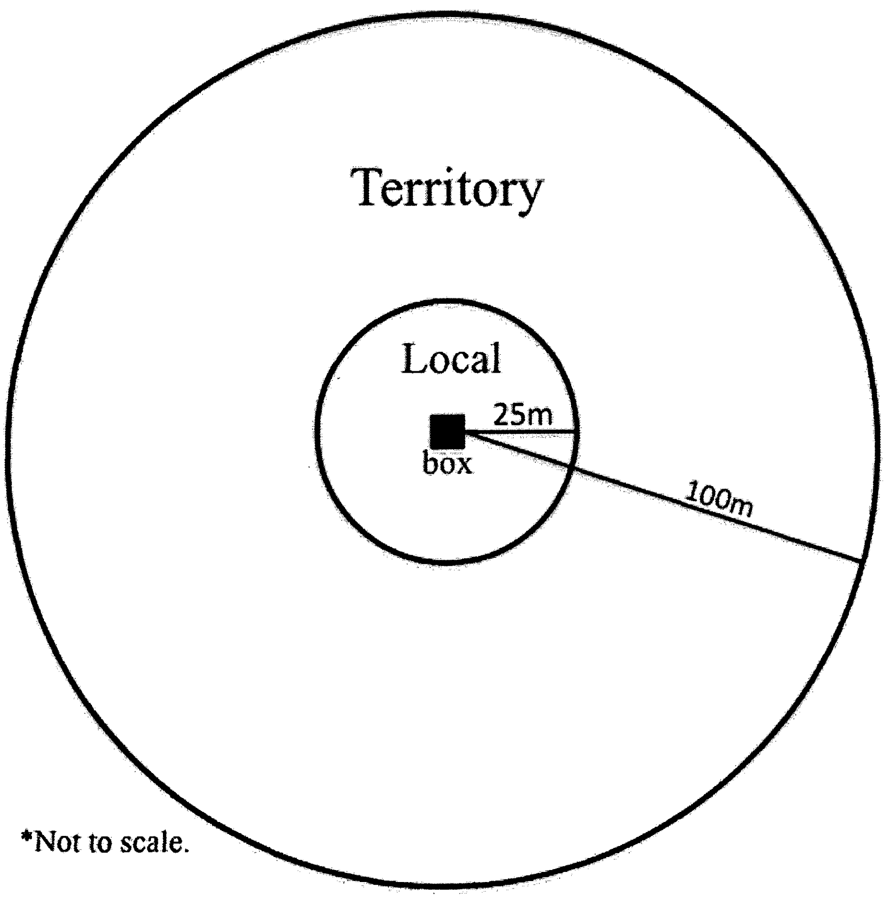

Figure 2. Box-centric scales: Local and Territory.

We measured landcover at the golf course scale by treating all of the territories within a golf site as a single space (Fig. 3). For example, a golf site had a single metric for the percent of forest it contained. Similarly, the response variables were consolidated from all nest boxes on a site: occupancy was the percentage of the available boxes occupied on a golf site, and reproductive parameters were the averages of all clutch sizes, hatching successes, and fledging successes for each golf site. This scale addressed whether the landcover available to bluebirds on a golf site as a whole related to overall occupancy or reproductive success of that golf site. The analysis focused on the population of birds at a golf site instead of breeding pairs as in the local and territory scales (n = 9 golf sites).

Finally, we defined the landscape scale as landcover within 1.5 km of the center of each golf site (about 7.07 km^2; Fig. 3). We determined the "center" of a golf site by drawing the smallest rectangle that would enclose all territories within a golf site, then calulating the geographical center of that rectangle. Landcover at larger scales has been shown to influence predator distributions, dispersal opportunities, and other ecological processes (Weins 1989; Whithers and Meentemeyer 1999). The landscape scale allowed us to determine whether habitat surrounding a golf site could predict bluebird occupancy and reproductive success within the site. Occupancy and reproductive success were summarized in the same way they were for the golf course scale. There were two golf sites that nearly bordered each other, so at this scale they were combined into one golf site (n = 8 golf sites).

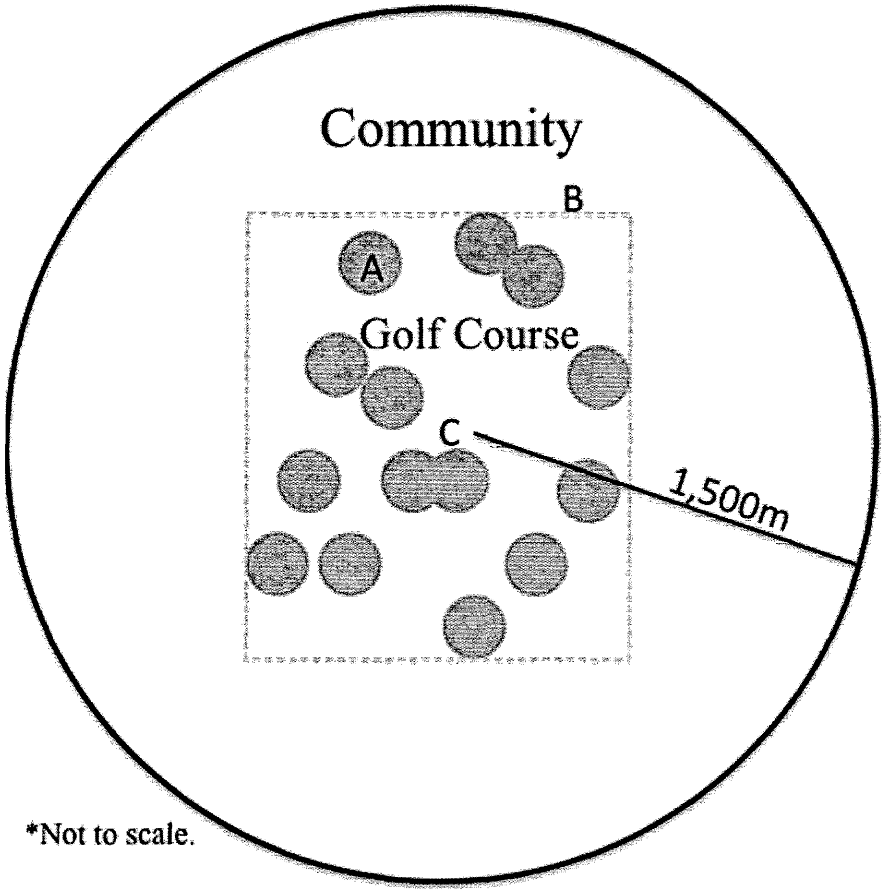

Figure 3. Site-centric scales: golf course and landscape. The golf course scale was the consolidation of all territories (A) within a golf site. The landscape scale was determined by creating a rectangle that touched the outer most territories (B); calculating the center of that rectangle (C), then creating a circle from that center with a 1,500-m radius.

Multi-scale studies involving songbirds usually focus on the scales between the territory scale (around 100-200-m radii), and a larger landscape scale (around 0.5-5-km radii), though some studies look at smaller "local" scales and intermediate "patch" scales (Hostetler and Knowles-Yanez 2003; Porter et al. 2005; Betts 2007; Luck and Korodaj 2008; Pennington et al. 2008; Cornell and Donovan 2009; Ryder 2010). Generally speaking, the four scales chosen for this study fall within the typical scale sizes of those used in the literature to look at avian diversity, occupancy, and reproductive success.

Habitat Characteristics

We acquired landcover data layers from an online database (U. S. Geological Survey 2010) and by digitizing satellite photographs by hand. For the community scale (7.07 km^2), we used 2001 digitized landcover data at a 30x30-m resolution from the Southeast Gap Analysis Project (U. S. Geological Survey 2010). In order to simplify the large list of landcover types, we reclassified them to match our digitized categories at the smaller scales (Table 1). Landscape scale landcover types were re-categorized into water, forest, wetlands, shrub-scrub, farmland, open-developed, and developed (Table 2).

There were no public data available for our golf sites detailed enough for the three smaller scales, ranging from 1,963 m^2 to 3,1416 m^2. Thus, we obtained aerial photographs taken in 2007 from local county authorities and digitized them by hand to a 1x1-m resolution using ArcGIS 9.3 (Environmental Research Institute 2006). We categorized landcover types as water, forest, mid-height vegetation, mowed grass, and vegetation-less cover (Table 3)..

We used FragStats (McGarigal et al. 2002) and FragStatsBatch 9 (Mitchell 2008a), to calculate the percent coverage of each landcover type, as well as the total amount of edge in meters within each landscape as a measure

Table 1. SEGAP landcover categories were reclassified into fewer categories for our analyses.

SEGAP Value and Category Name	Reclassified Landcover Type
Value 1: Open Water (fresh)	Water
Value 2: Open Water (Brackish/Salt)	Water
Value 35: Unconsolidated Shore (lake/river/pond)	Water
Value 4: Developed Open Space	Open-Developed
Value 145: Clearcut – Grassland/Herbacious	Open-Developed
Value 5: Low Intensity Developed	Developed
Value 6: Medium Intensity Developed	Developed
Value 7: High Intensity Developed	Developed
Value 18: Quarry/Strip Mine/Gravel Pit	Developed
Value 39: Atlantic Coastal Plain Dry and Dry-Mesic Oak Forest, or	Forest
Value 40: Atlantic Coastal Plain Mesic Hardwood and Mixed Forest	Forest
Value 71: Evergreen Plantations or Managed Pine (can include dense successional regrowth)	Forest
Value 148: Pasture/Hay	Farmland
Value 149: Row Crop	Farmland
Value 125: Successional Shrub/Scrub (Clear Cut)	Shrub/Scrub
Value 127:Successional Shrub/Scrub (Other)	Shrub/Scrub
Value 73: Atlantic Coastal Plain Northern Tidal Salt Marsh	Wetlands
Value 146:Herbaceous	Wetlands
Value 151: Atlantic Coastal Plain Blackwater Stream Floodplain Forest – Forest Modifier	Wetlands
Value 153: Atlantic Coastal Plain Small Blackwater River Floodplain Forest	Wetlands
Value 174: Atlantic Coastal Plain Northern Basin Swamp and Wet Hardwood Forest	Wetlands
Value 204: Atlantic Coastal Plain Northern Tidal Wooded Swamp	Wetlands
Value 215: Atlantic Coastal Plain Northern Fresh and Oligohaline Tidal Marsh	Wetlands
Value 248: Atlantic Coastal Plain Northern Tidal Salt Marsh	Wetlands

Table 2. Landcover types for the largest scale (Landscape) were acquired from 2001 pre-digitized data layers and reclassified to match smaller scales landcover types.

Large-Scale Landcover Type	Description
Water	Larger natural and man-made lakes, streams, and ponds.
Forest	Larger intact patches of evergreen, deciduous, and mixed forest.
Wetlands	Floodplain forest, swamp, and marsh.
Shrub-Scrub	Clear cut or other shrub-scrub
Farmland	Pasture, hay, and row crops.
Open-Developed	Open human-altered habitats such as golf courses, parks, and sparse neighborhoods. Note that all small-scale landcover types could be covered under this category.
Developed	Higher intensity development such as dense neighborhoods, cities, highways, and gravel pits.

Table 3. Landcover types for the three smaller scales (Golf Course, Territory, and Local) were digitized by hand from 2007 satellite photographs.

Small-Scale Landcover Type	Description
Water	Natural and man-made lakes, streams, and ponds.
Forest	Natural or manicured deciduous, evergreen, and mixed forest.
Mid-Height Vegetation (MidVeg)	Tall grasses that grew over 30 cm and rarely cut, shrubs of variable heights, small herbaceous and garden plants.
Mowed Grasses (Grass)	Grass kept below 10 cm, includes that tees, greens, and fairways of golf courses that were often kept below 2.5 cm.
Vegetation-less (Vegless)	Any area without vegetation, including large mud pits, sand traps, cart paths, roads, and buildings.

Occupancy and Reproductive Success

Prior to the beginning of this study, wooden nest boxes were constructed with 3.8 cm holes and placed on 1.5 m metal poles, except on one golf site where boxes were nailed to tree trunks. Most boxes also had predator guards in the form of galvanized stovepipe baffles or metal cone guards mounted on the poles supporting the nest boxes. The nest boxes on tree trunks had rectangular guards made of heavy wire mesh to keep predators from reaching into the boxes. Over time some boxes without predator guards were replaced with those with predator guards. The presence or absence of predator guards on each box was accounted for in our analyses.

Correlational Study Field Data

From 2007-2009, nest boxes were monitored every 4-7 days during the breeding season of March through August. Not every site was monitored every year: five sites were monitored three years, one site was monitored two years, and three sites were monitored one year. A box was considered "occupied" if eggs were present in a nest (n = 605 nests).

We recorded the number of eggs and nestlings, nestling ages, nest fate (failed or fledged), and reason for failure, if known. We recorded clutch size and brood size as the maximum number of eggs and nestlings observed, respectively, and the number of young fledged as the number of nestlings observed alive at the latest observation date. Only nestlings that were last observed at age 13 days or older were considered to have fledged. To avoid causing premature fledging, nests were monitored until nestlings were 15 days old, thereafter live nestlings were determined present by sound or by adult feeding behavior. If a nest was observed empty when nestlings would have been 16 days old or younger, then the nest was assumed to have failed due to predation. Clutch initiation dates were estimated when needed by using nestling ages to estimate hatch date, assuming 14 days of incubation, then counting back as many days as there were eggs, assuming one egg was laid per day. To avoid the complications of second or third broods influencing box success, we considered first broods only in our analyses by using nests with a clutch initiation date within 30 days of the earliest clutch initiation date of a season (n = 340).

We chose to investigate the relationship between landcover pattern and three measures of reproductive success: (1) clutch size; (2) hatching success (proportion of eggs that hatched); and (3) fledging success (proportion of eggs that fledged). Using multiple reproductive parameters helped to differentiate between stages of the nesting cycle where certain landcover types may play a greater or lesser role in influencing nesting and breeding.

Experimental Study Field Data

To test our findings from the correlational analysis, we conducted a field experiment in 2010 in which we relocated boxes to new areas of the golf sites and analyzed whether the observed relationships between landcover, occupancy, and reproductive success could be reproduced at new nesting sites. We chose three golf sites that shared the same box design and included the same predator guard. We relocated all boxes on these sites within one week in February, before the breeding season started.

We moved the boxes within 100-150 m from their original location to avoid bias associated with distance moved (n = 60 nest boxes). New locations had never previously contained nest boxes. Finally, we moved boxes to new areas that were structurally different in landcover from their original locations. These criteria presented nesting birds with a choice: 1) they could simply move to the box closest to where they nested in the previous year, or 2) they could find the box that more closely resembled favored habitat types. If the results showed the same relationships between landcover, occupancy, and reproductive success in the experiment as in the correlational study, this could be evidence that landcover truly was influencing these responses. Occupancy and reproductive data were collected in the same manner as the correlational study.

Statistical Analyses

Preliminary analyses revealed high correlation among landcover types. To account for this correlation and to reduce the number of variables in our models, we used principal components analysis (PCA, (Manly 1990) in SPSS statistical software (SPSS 1999) to produce composite explanatory variables that described the landscape. Each principal component (PC) represented a habitat gradient, where a score of zero represented an average amount of the measured landcover types given our data set, and a positive or negative score represented relatively more or less of certain habitat types. For example, a PC at the local scale assigned a more negative score to an area that had more forest, and a more positive score to an area with more grass. A local area that had a PC score of zero in this case would have the average amount of forest and grass, while a more positive score would have more grass and less forest. This analysis was conducted for each of the four scales separately, and included all boxes (or sites).

For the local and territory scales, we used an information-theoretic model-selection approach (Burnham and Anderson 2002) using SAS statistical software (SAS 2008) to evaluate univariate and additive linear models for the four avian response variables: occupancy, clutch size, hatching success and fledging success. We included two main effects that were known from previous analyses to affect bluebird productivity in all models: (1) annual variation ("year"); and (2) the presence or absence of a predator guard ("PG"). "Site" was used as a repeated measure. The "basic" model included only year, site, and predator guard and was present in each model set. This allowed us to compare how adding different landcover variables (PCs) explained variation in the occupancy and reproductive data. There were eight models in each set (Table 4), and a total of eight model sets were run in all. We considered models in a set to be influential with a $\Delta QIC\mu > 0.2$ (Manly 1990). The degree of support for each model within a set was determined using penalized quasi-likelihood information criterion ($QIC\mu$) and normalized model weights (w_i). The model in each set with the lowest QIC_μ value was considered to be the best fit to the observed data among the models evaluated. The model that carried all of the analytical weight ($\omega_i = 1.000$) was chosen as the best supported model. If the analytical weight was spread out among the different models, we model-averaged parameter estimates (Mitchell 2008b). Model averaging involves weighting beta values according to that model's overall weight in the set, then averaging the betas for each variable across all models in the set.

Table 4. Example model set for the local and territory scale analyses. The landcover variables (PCs) varied by scale. This model set was run for each of the four response variables at both the local and territory scales.

Model #	Parameters
1	Year + Site + PG ("Basic model")
2	Year + Site + PG + PC1
3	Year + Site + PG + PC2
4	Year + Site + PG + PC3
5	Year + Site + PG + PC1 + PC2
6	Year + Site + PG + PC1 + PC3
7	Year + Site + PG + PC2 + PC3
8	Year + Site + PG + PC1 + PC2 + PC3

We were limited in statistical power for the golf course and landscape scale because we only had nine and eight data points, respectively. We chose to simply plot the site-level response variables against each of the PCs for these scales, and used linear regression to test the relationships. We considered R^2 values at or above 0.300 as noteworthy relationships.

We also examined the extent of spatial autocorrelation in our data by examining Moran's I, generated in ArcGIS. This test measures whether spatial data are more or less likely to be correlated given their distance from one another. Resulting values can range from negative one (perfectly dispersed), to zero (random), to positive one (perfectly correlated). Appendix A reveals mixed results for our landcover variables. A majority of the variables were conclusively random, but some had varying degrees of being clustered. This may have created some bias in our results.

For the field experiment, data were only collected from three golf sites, so we only had large enough sample sizes to analyze the local and territory scales. Since the new box locations presented a new set of landcover data, we ran a new PCA with the landcover data from 2009 and 2010 for experimental boxes (n = 121). We wanted to know whether the change in the surrounding landcover of a box from one year to the next resulted in the expected change in our response variables based on the correlational analysis. We used simple linear regression to look for significant relationships and compared the findings to the correlational analysis.

RESULTS

Correlational Results

Principal Component Analysis

The principal components analysis generated three PCs with eigenvalues greater than one for each of the four spatial scales (Table 5). Collectively, the PCs explained 79%, 81%, 93% and 84% of the total landcover variation at local, territory, golf course, and landscape scales, respectively. The loading factors for each PC indicated significant correlation among original landcover variables.

Table 5. Principal components analysis loading factors, variable interpretations, and the percent of explained variation for each landcover variable at each scale.

Variables	PC1	PC2	PC3
Local (n=288)			
Grass	-0.167	0.604	-0.757
MidVeg	-0.134	0.269	0.938
Water	0.11	0.313	0.023
Vegless	0.928	0.018	-0.062
Forest	0.007	-0.988	-0.042
Edge	0.917	0.163	0.02
Interpretation	more fragmented barren land	more grass, less forest	more shrub, less grass
% Total Variance	23.90%	25.70%	24.30%
Territory (n=288)			
Grass	0.09	-0.899	0.328
MidVeg	0.063	0.786	0.245
Water	-0.177	0.152	.0.725
Vegless	0.93	0.03	-0.117
Forest	-0.39	0.327	-0.803
Edge	0.924	-0.042	0.135
Interpretation	more fragmented barren land	more shrub, less grass	more water, less forest
% Total Variance	31.90%	26.00%	22.80%
Golf Course (n=9)			
Grass	-0.877	0.322	-0.313
MidVeg	-0.783	0.23	0.412
Water	0.661	0.691	0.179
Vegless	0.715	-0.138	-0.603
Forest	0.437	-0.719	0.538
Edge	0.532	0.785	0.236
Interpretation	more forested edge, less open land	more fragmented barren land, less shrub	more shrub, less forest
% Total Variance	33.5%	31.0%	28.8%
Landscape (n=8)			
ShrubScrub	-0.463	0.411	0.649
Water	0.481	0.62	-0.556
Forest	-0.737	0.589	0.15
Agriculture	-0.751	-0.38	-0.362
Wetlands	0.721	0.554	-0.331
Developed	0.722	-0.584	0.007
Open_Developed	0.694	0.121	0.432
Edge	0.745	-0.028	0.456
Interpretation	more urban, less agricultural/wooded	more wetland/forest, less highly developed	more shrub/scrub, less water
% Total Variance	31.2%	28.4%	24.4%

At the local scale (n = 288), high scores of PC1 reflected higher amounts of edge and vegetation-less cover. High scores of PC2 reflected higher amounts of forest and lower amount of grass. High scores of PC3 reflected higher amount of mid-height vegetation and lower amounts of grass. Hence, we have named these PCs according to these primary loading factors: local PC1 as *more fragmented barren land*; local PC2 as *more grass, less forest*; and local PC3 as *more shrub, less grass* (Table 6).

At the territory scale (n=288), higher scores of PC1 reflected high amounts of edge and vegetation-less cover. High scores of PC2 reflected higher amounts of mid-height vegetation and lower amounts of grass. High scores of PC3 reflected higher amounts of water and lower amounts of forest. We thus named territory PC1 as *more fragmented barren land*, territory PC2 as *more shrub, less grass*, and territory PC3 as *more water, less forest* (Table 6).

At the golf course scale, high scores of PC1 reflected higher amounts of forest, vegetation-less cover, edge, and mid-height vegetation, with lower amounts of grass and water. High scores of PC2 relfected higher amounts of edge and vegetation-less cover with lower amounts of mid-height vegetation. High scores of PC3 reflected higher amounts of mid-height vegetation and lower amounts of forest. Therefore, we named golf course scale PC1 as *more forested edge, less open land*, golf course scale PC2 as *more fragmented barren land, less shrub*, and golf course scale PC3 as *more shrub, less forest* (Table 6).

At the landscape scale, high scores of PC1 reflected higher amounts of edge, wetlands, developed, and open-developed land, with lower amounts of forest and agricultural land. High scores of PC2 reflected higher amounts of water, forest, and wetlands with lower amounts of developed land. High scores of PC3 reflected higher amounts of shrub-scrub and lower amounts of water. Thus, we renamed landscape scale PC1 as *more urban, less agricultural/wooded*, landscape scale PC2 as *more wetland/forest, less highly developed*, and landscape scale PC3 as *more shrub/scrub, less water* (Table 6).

Table 6. Principal components analysis variable summary.

PC		Interpretations
Local		
	PC1	more fragmented barren land
	PC2	more grass, less forest
	PC3	more shrub, less grass
Territory		
	PC1	more fragmented barren land
	PC2	more shrub, less grass
	PC3	more water, less forest
Golf Course		
	PC1	more forested edge, less open land
	PC2	more fragmented barren land, less shrub
	PC3	more shrub, less forest
Landscape		
	PC1	more urban, less agricultural/wooded
	PC2	more wetland/forest, less highly developed
	PC3	more shrub/scrub, less water

General Occupancy and Reproductive Statistics

From 2007-2009 we monitored nine golf sites with a total of 605 boxes containing a total of 344 nests (Table 7). The percent of boxes occupied ranged from 21-88% on golf sites with an average of 60% of boxes occupied over the three years. The average clutch size on sites ranged from 4.32 – 4.80 eggs per nest with an overall average of 4.55 eggs per nest. Hatching success ranged from 57-95% on sites, with an overall average of 75% of eggs hatched. This is lower than the reported 83% hatching success for the species (Gowaty and Plissner 1998). Fledging success ranged from 35-95%, with an overall average of 58% eggs that produced fledglings. Brood survival (the percentage of hatchlings that fledged) ranged from 60-100% with an overall average of 73%, which is within the normal range of 75-90% for the species (Gowaty and Plissner 1998). Finally, nest success (the percentage of nests that produced at least one fledgling) ranged from 44-100%, with an overall average of 62%, which is also within the normal range of 55-84% (Gowaty and Plissner 1998).

Table 7. Occupancy and reproductive statistics for all years of the correlational study. Brood survival and nest success are included to compare to previous literature.

Site	# Boxes	# Nests	% Boxes Occupied	Avg. Clutch Size	Avg. % Hatched	Avg. % Fledged	Brood Survival	Nest Success
1	39	24	61.54	4.38	72.29	63.13	87.37	70.83
2	24	5	20.83	4.80	95.00	95.00	100.00	100.00
3	175	72	41.14	4.65	57.30	34.80	61.30	44.12
4	60	41	68.33	4.63	85.00	63.29	75.70	73.17
5	25	17	68.00	4.41	71.18	58.24	82.50	70.59
6	103	47	45.63	4.64	75.14	53.30	72.63	63.83
7	48	42	87.50	4.55	60.60	36.15	59.61	45.24
8	56	37	66.07	4.32	75.00	45.54	63.03	56.76
9	75	59	78.67	4.61	82.71	71.19	85.53	81.36
All	605	344	59.75	4.55	74.91	57.85	73.09	62.35

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Model Selection & Regression Results

Occupancy

At the local scale, all univariate landcover models were supported (Table 8). However, the model-averaged betas were small and highly variable, with 95% confidence intervals spanned zero in near symmetric patterns (Table 10; Appendix B). At the territory scale, the three supported models all contained "more shrub, less grass" (PC2), with the univariate PC2 model carrying about double the weight of the other two (Table 9). Among the model averaged beta values, this was the only one to vary almost entirely within the negative values (β = -0.238, 95% CI = -0.496-0.021), indicating that birds were more likely to occupy territories with more mowed grass and less mid-height vegetation (Table 11).

Moving from the box-centric scales to the site-centric scales, the proportion of boxes occupied on a golf site was not influenced by any landcover variable (PC1: β = -0.060, R^2 = 0.094; PC2: β = 0.040, R^2 = 0.040; PC3: β = -0.100, R^2 = 0.217). At the larger landscape scale, a higher proportion of boxes were occupied on golf courses surrounded by more agricultural and forest and less urban land (PC1: β = -0.140; R^2 = 0.416). The other landscape variables describing gradients from more forest/wetlands to mildly developed space, and more water to more shrub/scrub, were not related to the percent of occupied boxes (PC2: β = 0.034; R^2 = 0.024; PC3: β = -0.070; R^2 = 0.103).

Clutch Size

At the local scale, the univariate model containing "more grass, less forest" (PC2) received all of the weight in the data, so there was no need to average the models (Table

8). Boxes had larger clutch sizes when they were locally surrounded by more grass and less forest (β = 0. 018, 95% CI = -0.005-0.041). The territory scale also had a single model that received all the weight in the data, containing the variable "more water, less forest" (PC3; Table 9). The beta value, however, was small and highly variable (β = 0. 008, 95% CI = -0.025-0.041).

At the golf course scale, there were larger average clutch sizes on golf sites containing more forested edge with less open land (PC1: $\beta = 0.083$; $R^2 = 0.315$), but the other habitat variables were not influential (PC2: $\beta = -0.06$; $R^2 = 0.159$; PC3: $\beta = 0.076$; $R^2 = 0.262$). At the landscape scale, there were no landcover variables related to clutch size (PC1: $\beta = 0.053$; $R^2 = 0.339$; PC2: $\beta = -0.089$; $R^2 = 0.743$; PC3: $\beta = 0.052$; $R^2 = 0.126$).

Hatching Success

At the local scale, all univariate landcover models were similarly supported (Table 8). "More fragmented barren land" (PC1) was highly variable, but had a comparatively large beta value (β = 0. 100, 95% CI = -0.190-0.390), suggesting that there was higher hatching success in boxes locally surrounded by more fragmented barren land (Table 10; Appendix B). The other local variables were smaller and more variable across zero. At the territory scale, all univariate landcover variables were also similarly supported (Table 9), but all beta values were small and highly variable (Table 11).

At the golf course scale, only "more forested edge, less open land" had an acceptable correlation with hatching success (PC1: $\beta = 0.072$, $R^2 = 0.389$), with higher hatching success on courses with more forested edge and less open space. The other landcover variables were not considered good predictors of hatching success (PC2: β = 0.046, $R^2 = 0.159$; PC3: β = 0.040, $R^2 = 0.118$). At the landscape scale, no landcover variables were appropriate predictors of hatching success (PC1: β = 0.059, $R^2 = 0.089$; PC2: β = 0.018, $R^2 = 0.009$; PC3: β = 0.002, $R^2 < 0.001$).

Fledging Success

At the local scale, the univariate models containing "more fragmented barren land" (PC1) and "more shrub, less grass" (PC3) were supported (Table 8), but the beta values were small and highly variable (Table 10; Appendix B). At the territory scale, four out of the seven habitat models were supported (Table 9). Models containing "more fragmented barren land" (PC1) and "more shrub, less grass" (PC2) received more weight than "more water, less forest" (PC3). Though the beta values are highly variable, they are comparatively strong for PC1 and PC2, suggesting that there was higher fledging success on territories with more fragmented barren land, and on territories with more grass and less shrub (Table 11).

At the golf course scale, there was higher fledging success on golf sites containing more forested edge and less open land (PC1: β = 0.136, $R^2 = 0.525$). The other two golf course scale landcover variables were not important in explaining fledging success (PC2: β = 0.018, $R^2 = 0.009$; PC3: β = 0.035, $R^2 = 0.034$). Finally, at the landscape scale, there were no landcover variables that correlated strongly to fledging success (PC1: β = 0.059, $R^2 = 0.089$; PC2: β = 0.018, $R^2 = 0.009$; PC3: β = 0.002, $R^2 < 0.001$

Table 8. Simplified models of occupancy, clutch size, hatching success, and fledging success at the local scale for Eastern Bluebirds living on golf courses near Williamsburg, Virginia from 2007-2009. Supported models are bolded ($\Delta QIC\mu<2$).

Response Variable	Models[a]	K[b]	$QIC\mu$[c]	$\Delta QIC\mu$[d]	ω_i[e]
Occupancy	**Basic**	**5**	**758.875**	**0.000**	**0.283**
	PC1	**6**	**759.921**	**1.045**	**0.168**
	PC2	**6**	**760.732**	**1.857**	**0.112**
	PC3	**6**	**759.927**	**1.051**	**0.168**
	PC1 + PC2	7	761.845	2.969	0.064
	PC1 + PC3	7	760.931	2.056	0.101
	PC2 + PC3	7	761.818	2.943	0.065
	PC1 + PC2 + PC3	8	762.882	4.006	0.038
Clutch Size	Basic	5	-9599.787	46.279	0.000
	PC1	6	-9566.129	79.937	0.000
	PC2	**6**	**-9646.066**	**0.000**	**1.000**
	PC3	6	-9569.307	76.759	0.000
	PC1 + PC2	7	-9612.414	33.651	0.000
	PC1 + PC3	7	-9535.815	110.250	0.000
	PC2 + PC3	7	-9615.670	30.395	0.000
	PC1 + PC2 + PC3	8	-9582.203	63.862	0.000
Hatching Success	**Basic**	**5**	**151.300**	**0.000**	**0.295**
	PC1	**6**	**152.343**	**1.043**	**0.175**
	PC2	**6**	**152.997**	**1.698**	**0.126**
	PC3	**6**	**152.719**	**1.420**	**0.145**
	PC1 + PC2	7	154.025	2.725	0.076
	PC1 + PC3	7	153.780	2.481	0.085
	PC2 + PC3	7	154.436	3.137	0.061
	PC1 + PC2 + PC3	8	155.496	4.196	0.036
Fledging Success	**Basic**	**5**	**146.296**	**0.000**	**0.300**
	PC1	**6**	**147.703**	**1.407**	**0.149**
	PC2	6	148.491	2.195	0.100

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PC3	**6**	**147.040**	**0.745**	**0.207**
PC1 + PC2	7	149.940	3.645	0.049
PC1 + PC3	7	148.488	2.193	0.100
PC2 + PC3	7	149.361	3.066	0.065
PC1 + PC2 + PC3	8	150.862	4.566	0.031

[a]Model structure: Basic model included year, the presence of a predator guard, and site as a repeated measure. The other "habitat" models included the variables of the intercept model, plus the PC habitat variables derived for this scale: PC1=more fragmented barren land; PC2=more grass, less forest; PC3=more shrub, less grass.
[b]K is the number of parameters.
[c]Penalized quasi-likelihood information criteria generated with Generalized Estimating Equations; best model has lowest value.
[d]Scaled QICμ; best model has ΔQICμ = 0
[e]Model weight, interpreted as a probability.

Table 9. Simplified models of occupancy, clutch size, hatching success, and fledging success at the territory scale for Eastern Bluebirds living on golf courses near Williamsburg, Virginia in 2007-2009. Supported models are bolded (ΔQICμ<2).

Response Variable	Models[a]	K[b]	QICμ[c]	ΔQICμ[d]	ω_i[e]
Occupancy	Basic	5	758.875	3.116	0.076
	PC1	6	760.809	5.049	0.029
	PC2	**6**	**755.760**	**0.000**	**0.362**
	PC3	6	760.218	4.459	0.039
	PC1 + PC2	**7**	**756.968**	**1.208**	**0.198**
	PC1 + PC3	7	762.197	6.438	0.014
	PC2 + PC3	**7**	**757.064**	**1.304**	**0.189**
	PC1 + PC2 + PC3	8	758.470	2.711	0.093
Clutch Size	Basic	5	-9599.787	57.066	0.000
	PC1	6	-9569.420	87.433	0.000
	PC2	6	-9579.294	77.559	0.000
	PC3	**6**	**-9656.853**	**0.000**	**1.000**
	PC1 + PC2	7	-9547.136	109.717	0.000
	PC1 + PC3	7	-9622.668	34.185	0.000

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	PC2 + PC3	7	-9635.876	20.978	0.000
	PC1 + PC2 + PC3	8	-9602.619	54.235	0.000
Hatching Success	**Basic**	**5**	**151.300**	**0.000**	**0.338**
	PC1	**6**	**153.188**	**1.888**	**0.131**
	PC2	**6**	**152.658**	**1.359**	**0.171**
	PC3	**6**	**153.113**	**1.814**	**0.137**
	PC1 + PC2	7	154.533	3.233	0.067
	PC1 + PC3	7	154.857	3.558	0.057
	PC2 + PC3	7	154.465	3.165	0.069
	PC1 + PC2 + PC3	8	156.217	4.917	0.029
Fledging Success	**Basic**	**5**	**146.296**	**0.000**	**0.207**
	PC1	**6**	**146.417**	**0.121**	**0.195**
	PC2	**6**	**146.867**	**0.571**	**0.156**
	PC3	**6**	**147.882**	**1.587**	**0.094**
	PC1 + PC2	**7**	**147.279**	**0.984**	**0.127**
	PC1 + PC3	**7**	**147.897**	**1.601**	**0.093**
	PC2 + PC3	7	148.482	2.186	0.070
	PC1 + PC2 + PC3	8	148.834	2.539	0.058

[a]Model structure: Basic model included year, the presence of a predator guard, and site as a repeated measure. The other "habitat" models included the variables of the intercept model, plus the PC habitat variables derived for this scale: PC1=more fragmented barren land; PC2=more shrub, less grass; PC3=more water, less forest.
[b]K is the number of parameters.
[c]Penalized quasi-likelihood information criteria generated with Generalized Estimating Equations; best model has lowest value.
[d]Scaled QICμ; best model has ΔQIC$\mu = 0$
[e]Model weight, interpreted as a probability.

Table 10. Model-averaged parameter estimates and upper and lower 95% confidence intervals for the local scale. For clutch size, only information from the single supported model is provided.

Response Variable	Predictor Variable	β	95%LowerCL	95%HighCL
Occupancy	more fragmented barren land	0.044	-0.165	0.254

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	more grass, less forest	0.011	-0.112	0.135
	more shrub, less grass	-0.045	-0.241	0.151
Clutch Size				
	more grass, less forest	0.018	-0.005	0.041
Hatching Success	more fragmented barren land	0.1	-0.19	0.39
	more grass, less forest	-0.025	-0.142	0.093
	more shrub, less grass	-0.01	-0.188	0.169
Fledging Success	more fragmented barren land	0.018	-0.163	0.200
	more grass, less forest	-0.036	-0.206	0.134
	more shrub, less grass	-0.067	-0.342	0.209

Table 11. Model-averaged parameter estimates and upper and lower 95% confidence intervals for the terriotry scale. For clutch size, only information from the single supported model is provided.

Response Variable	Predictor Variable	β	95%LowerCL	95%HigherCL
Occupancy	more fragmented barren land	-0.029	-0.19	0.132
	more shrub, less grass	-0.238	-0.496	0.021
	more water, less forest	-0.023	-0.152	0.106
Clutch Size				
	more water, less forest	0.008	-0.025	0.041
Hatching Success	more fragmented barren land	0.028	-0.097	0.153
	more shrub, less grass	-0.037	-0.214	0.141
	more water, less forest	0.008	-0.088	0.103
Fledging Success	more fragmented barren land	0.099	-0.136	0.334
	more shrub, less grass	-0.107	-0.407	0.194
	more water, less forest	-0.025	-0.146	0.096

The Effect of Predator Guards

Boxes without predator guards were 14% less likely to be occupied, had clutch sizes that were smaller by 0.23 eggs, had 18% lower hatching success and 22% lower fledging success compared to boxes with predator guards. Within the model selection, all beta values were in the negative range (Appendix C).

Experimental Results

Principal Components Analysis

We ran a PCA on the landcover surrounding 60 relocated boxes. There were three PCs with eigenvalues greater than one for both the local and territory scales of analyses. Collectively, the PCs explained 82% and 81% of the total landcover variation at local and territory scales, respectively (Table 12). Landcover variables were highly correlated.

Table 12. Field experiment principal component analysis using landoover data for experimental boxes from 2009 and 2010. Loading factors, variable interpretations, and percent of explained variation are provided.

Variables	PC1	PC2	PC3
Local (n=60)			
Grass	.329	.891	-.009
MidVeg	-.351	-.475	-.800
Water	-.148	.399	-.037
Vegless	.886	-.217	.148
Forest	-.220	-.402	.867
Edge	.836	.259	-.130
Interpretation	more fragmented barren land	more grass	more forest, less shrub
% Total Variance	36.072	24.347	17.459
Territory (n=60)			
Grass	.727	.354	-.165
MidVeg	-.114	-.990	-.068
Water	.009	.050	.997
Vegless	.820	.134	-.041
Forest	-.888	.318	-.145
Edge	.819	.150	.061
Interpretation	more development, less forest	less shrub	more water
% Total Variance	45.720	19.672	17.511

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At the local scale, high scores of PC1 reflected higher amounts of edge and vegetation-less land, high scores of PC2 reflected higher amounts of grass, and high scores of PC3 reflected higher amounts of forest and lower amounts of mid-height vegetation. Hence, we named local PC1 as *more fragmented barren land*; local PC2 as *more grass*; and local PC3 as *more forest, less shrub* (Table 13).

At the territory scale, high scores of PC1 reflected higher amounts of edge, vegetation-less land, and grass with lower amounts of forest. High scores of PC2 reflected lower amounts of mid-height vegetation. High scores of PC3 reflected higher amounts of water. We thus named territory PC1 as *more development*, territory PC2 as *less shrub*, and territory PC3 as *more water* (Table 13).

Table 13. Field experiment principal component analysis variable summary.

Habitat Variable		Interpretations
Local		
	PC1	more fragmented barren land
	PC2	more grass
	PC3	more forest, less shrub
Territory		
	PC1	more development, less forest
	PC2	less shrub
	PC3	more water

Linear Regression Results

Using p = 0.05 as our cut-off for significance, there were three important landcover variables: "more grass" at the local scale, "more grass" at the territory scale, and "more development, less forest" at the territory scale (Table 14).

Table 14. Field experiment results from linear regression analysis. Bolded variables are significant ($p \leq 0.5$).

Scale	Response	PC	β	SE	p-value
Local	Occupancy	more forest, less shrub	-0.231	0.182	0.206
		more fragmented barren land	0.344	0.232	0.138
		more grass	-0.053	0.191	0.781
	Clutch Size	more forest, less shrub	-0.042	0.154	0.787
		more fragmented barren land	0.059	0.169	0.731
		more grass	-0.043	0.169	0.800
	Hatching Success	more forest, less shrub	-0.004	0.066	0.954
		more fragmented barren land	0.108	0.070	0.132
		more grass	**0.144**	**0.068**	**0.041**
	Fledging Success	more forest, less shrub	0.075	0.073	0.311
		more fragmented barren land	-0.018	0.081	0.821
		more grass	**0.201**	**0.073**	**0.009**
Territory	Occupancy	less shrub	-0.472	0.341	0.165
		more development, less forest	0.411	0.307	0.180
		more water	0.123	0.335	0.714
	Clutch Size	less shrub	-0.094	0.202	0.645
		more development, less forest	**-0.502**	**0.228**	**0.035**
		more water	0.036	0.324	0.912
	Hatching Success	less shrub	0.024	0.086	0.781
		more development, less forest	0.057	0.104	0.583
		more water	0.020	0.138	0.886
	Fledging Success	less shrub	0.143	0.093	0.136
		more development, less forest	0.145	0.114	0.211
		more water	0.160	0.152	0.302

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Occupancy

There were no significant relationships between landcover variables and occupancy at the local or territory scale.

Clutch Size

There were no significant relationships between landcover and clutch size at the local scale. However, nest boxes that were moved to territories with less development had larger clutch sizes compared to the previous year (Fig. 4).

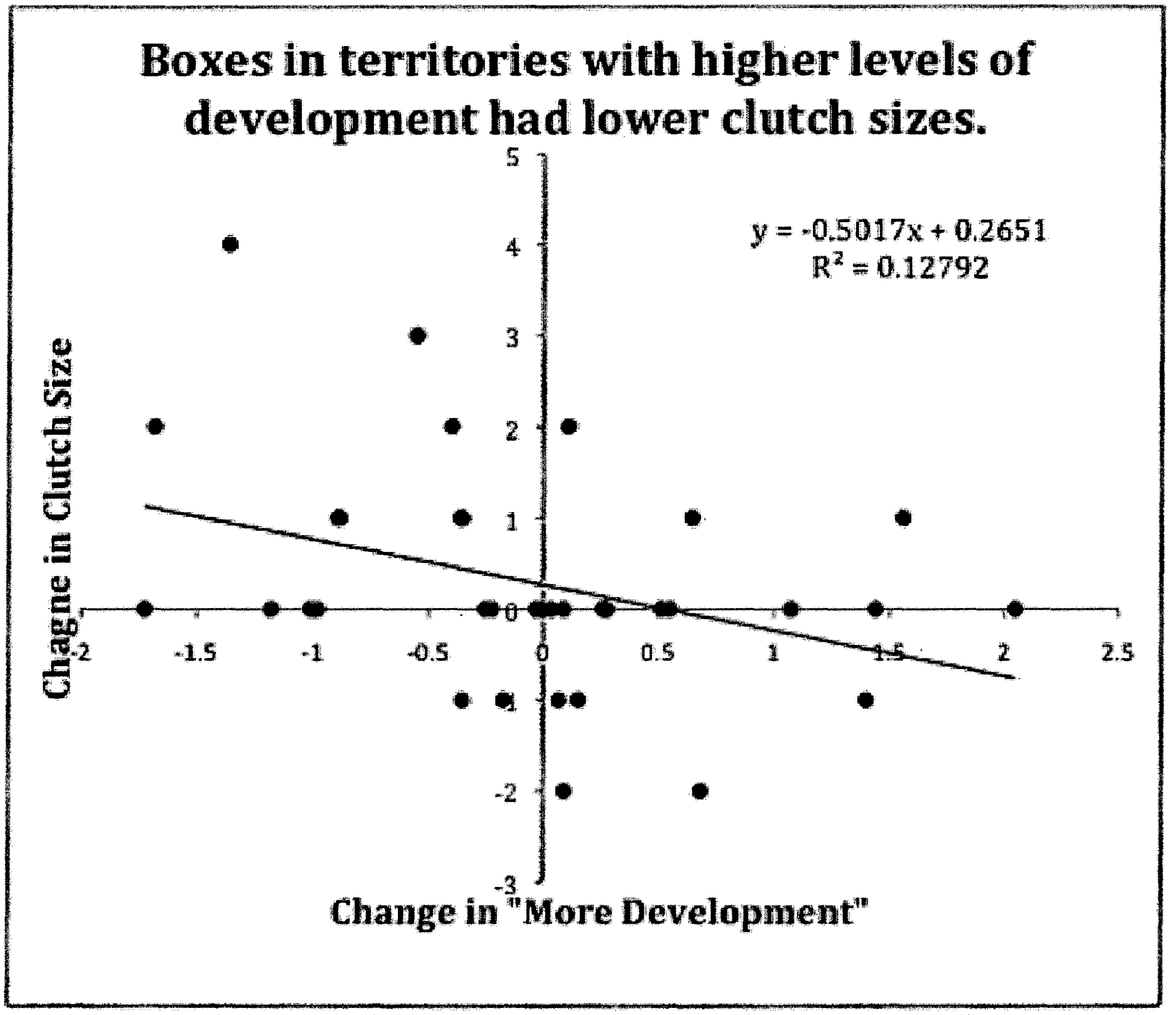

Figure 4. Change in the amount of developed land and the corresponding change in clutch size for relocated nest boxes between 2009 and 2010.

Hatching success

At the local scale, nest boxes that were moved to areas with more grass had increased, hatching success compared to the previous year (Fig. 5).

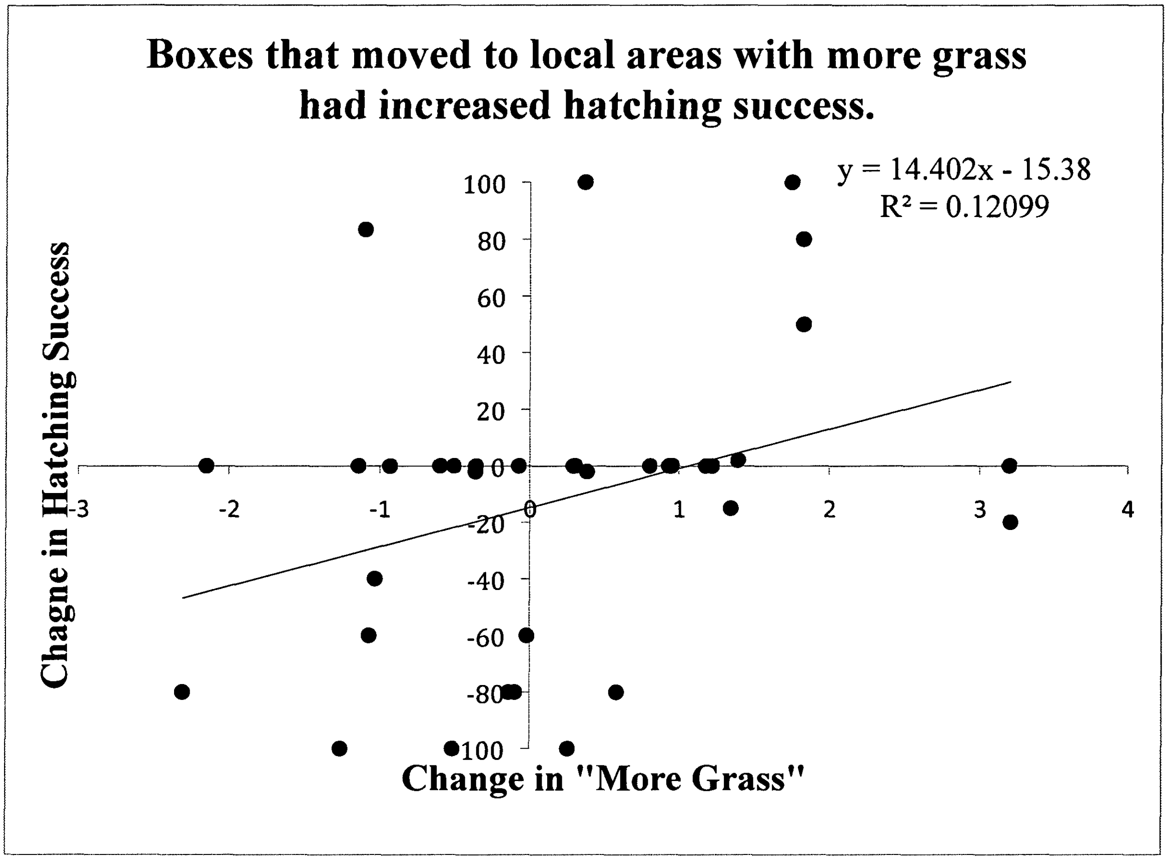

Figure 5. Change in the amount of grass and the corresponding change in hatching success for relocated nest boxes between 2009 and 2010.

Fledging success

Also at the local scale, when boxes were moved to areas with more grass they had increased fledging success compared to the previous year (Fig. 6).

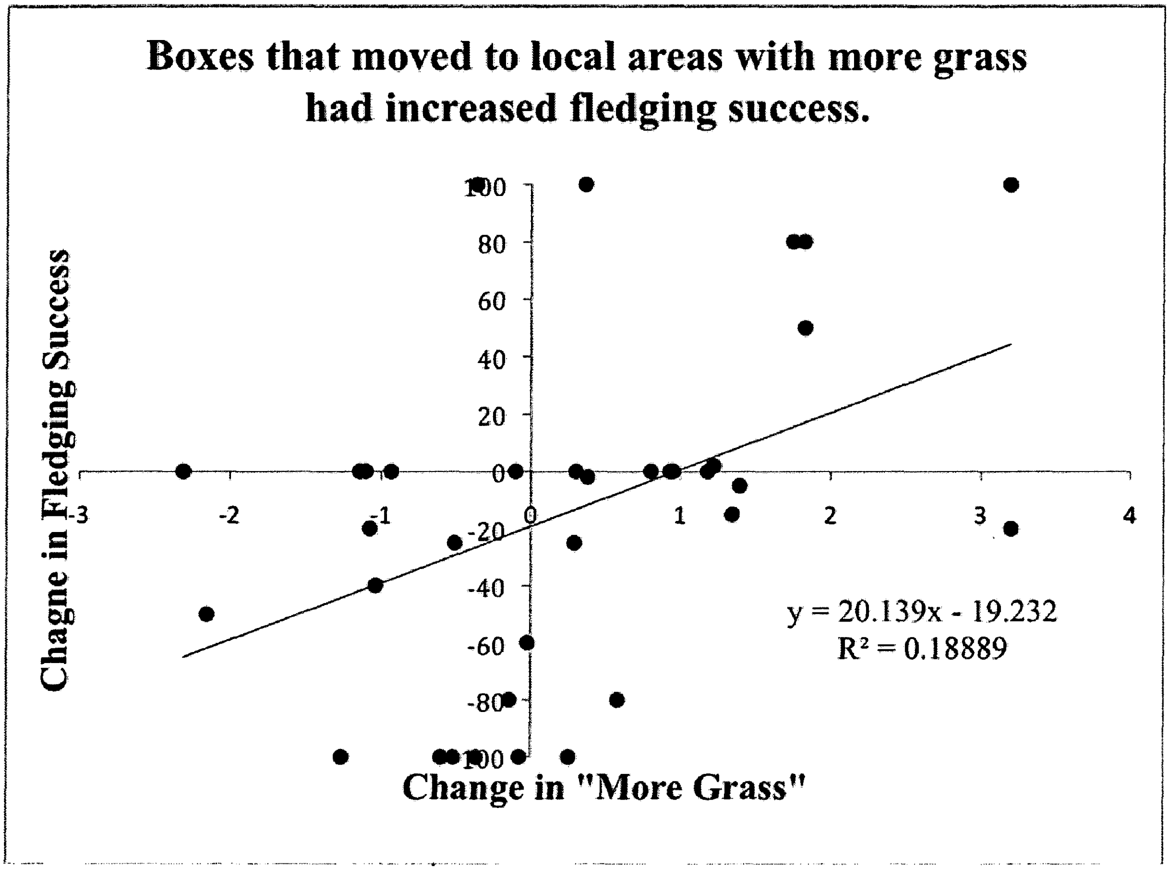

Figure 6. Change in the amount of grass and the corresponding change in fledging success for relocated nest boxes between 2009 and 2010.

Results Summary

Birds were more likely to nest in boxes that were on territories with more grass and less shrub. Golf sites had a higher percentage of their boxes occupied when the surrounding landscape had more agriculture and forest with less urban land. There were larger clutch sizes in boxes that were locally surrounded by more grass with less forest, and were on territories with more forest with less development. Golf sites with more forested edge and less open land had higher average clutch sizes. Both hatching success and fledging success were higher in boxes that were locally surrounded by more grass. The average percentage of eggs that hatched per box, as well as the average percentage of eggs that produced fledglings per box, were higher on golf sites that contained more forested edge with less open land (Table 15).

The box relocation experiment generally supported our predictions at the local scale, but provided different results at the territory scale (Table 15). Moving nest boxes to areas where they were locally surrounded by more grass did increase the box's reproductive success as expected. At the territory scale, it was predicted that moving a boxes to territories with more grass and less shrub would increase their likelihood of being occupied, but the field experiment revealed no relationships between landcover and occupancy. We did not expect to see a relationship between landcover and reproductive success at the territory scale, but instead found that boxes moved to territories with more forest and less development responded with increased clutch sizes.

Table 15. Results summary for the entire study. Experimental results are gray and italicized. Relevant statistics are provided. "CI" represents 95% confidence intervals.

	SCALE	RESPONSE							
		Occupancy		Clutch Size		Hatching Success		Fledging Success	
BOX-CENTRIC	Local			more grass, less forest	*$\beta = 0.018$* CI: -0.005-0.041	*more grass*	*$\beta = 0.201$ $p = 0.041$*	*more grass*	*$\beta = 0.073$ $p = 0.009$*
BOX-CENTRIC	Territory	more shrub, less grass	*$\beta = -0.238$* CI: -0.496-0.021	*more development, less forest*	*$\beta = -0.502$ $p = 0.035$*				
SITE-CENTRIC	Golf Course			more forested edge, less open land	$\beta = 0.083$ $R^2 = 0.315$	more forested edge, less open land	$\beta = 0.072$ $R^2 = 0.389$	more forested edge, less open land	$\beta = 0.136$ $R^2 = 0.525$
SITE-CENTRIC	Community	more urban, less agriculture/ woods	$\beta = -0.140$, $R^2 = 0.416$						

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Discussion

Limitations

Because the analyses addressed only correlations between landcover, occupancy, and reproductive success, we can only speculate about the mechanisms responsible for these relationships. Due to limited time and resources, we did not have a large enough sample size to run a model analysis or experimental regression on the golf course and landscape scales. Multiple people recorded field data over the years in different ways, so though we did our best to accurately combine all years of data, there could be varying reliability/comparability. We were limited by the variation present on the golf sites in our study, which was more of a problem at the two larger scales. The average amount of individual landcover type variation at the smaller scales was 68%, while the average amount of landcover variation at the larger scales was only 18%. A wider range of golf course habitats and their surrounding landscapes may have resulted in stronger relationships. In addition, some golf courses had areas of neighborhood construction that changed the landcover over the years. Satellite photos were taken in 2007 but digitize to more closely match landcover in 2009 when possible. Having digitized landcover that was specific to each individual year may have provided more accurate or stronger results, at least for the smaller scales.

Landcover and Occupancy

When a bluebird is flying over a large landscape looking for an area to search for nest sites, they are likely looking for landscapes that most closely match the kind of habitat they evolved to utilize – forest edges bordering open fields or clearings. This could explain why golf courses that were surrounded by more agriculture and forest, and less urban areas had a higher percentage of occupied boxes. Once on a golf site, the birds may have chosen territories with more grass and less shrub because shorter grass allows for easier sightings of insect prey, and thus higher foraging efficiency.

Landcover and Reproduction

Clutch size appeared to be the most "affected" response variable, as there was influential landcover at the local, territory, and golf course scales. Larger clutch sizes were correlated with more grass around a box, less development on territories, and more fragmented patches of forest on golf courses as opposed to large patches of open space. Females may have laid more eggs when there was more grass close to box if grass is an indicator of more food or higher foraging efficiency. It is also possible that higher quality birds (more healthy and perhaps more competitive) may have chosen nesting sites where they could easily forage close to the box, and also be able to more easily notice approaching predators. The field experiment supported an unexpected correlation between larger clutch sizes and territories with more forest and less development (often in the form of neighborhoods bordering fairways). Neighborhoods create disturbances in the form of people, cars, and noise. High levels of such disturbance has been linked to lower bluebird reproductive success (Kight and Swaddle 2007). As mentioned above, higher quality birds may have chosen territories with less development and more natural (forested) habitat. Golf courses had larger average clutch sizes when they contained more fragmented forest and less open space. If the birds are taking cues from landcover at this larger spatial extent, then perhaps they are willing to expend more energy in egg laying when more forest in the area can provide cover from avian predators, perches for foraging, and a greater availability of alternate breeding sites.

Hatching success reflects parental health, incubating behavior, and nest defense during the incubation stage of breeding. Boxes that were relocated to local areas with more grass experienced increased hatching success, perhaps due to easier foraging for both parents and better detection of ground predators. Golf sites with more fragmented patches of forest had a higher percentage of hatched eggs than sites with more open land (grass and water). The availability of many patches of forest distributed throughout a site may provide more perches for easier foraging, and more cover for hiding or escaping from avian predators (namely hawks). With easier foraging and a greater chance of keeping both parents alive, the eggs were more likely to be properly incubated and hatch successfully.

Fledging success may be the most important measure of the in-nest breeding cycle, as it represents how much of the initial female energy investment (clutch size) resulted in birds that lived to fledge from the nest and potentially contribute to the next generation. Laying many eggs is not a useful reproductive strategy if those embryos never survive to leave the box. The same landcover that influenced hatching success also influenced fledging success in the same way, but with stronger relationships. Again, boxes that were relocated to local areas with more grass experienced increased fledging success. It is not surprising that the benefit of easy foraging is more important at this stage, when the parents are working their hardest to feed older chicks with large appetites. The ability to forage very close to the nest box is much less energy-consuming and less dangerous than having to fly back and forth to more distant parts of the territory. And again, golf sites with more fragmented patches of forest likely provided more efficient foraging and more protection from predators, leading to increased fledging success.

How effective was the experiment?

The field experience was more successful in confirming our predictions at the local than at the territory scale. Though there were no direct confirmations for any one specific response variable, collapsing the reproductive parameters into a single category allowed a more comprehensive view of the results (Table 16). Local scale occupancy predicted no habitat relationships, and none were found in the field experiment. The correlational analyses predicted higher occupancy for territories with more grass and less shrub, but no significant relationships were found in the experiment analysis. In general, it was predicted that more grass and less forest immediately around a box would result in higher reproductive success, and this was confirmed by the experiment. However, though there were no predicted relationships between landcover and reproductive success at the territory scale, the experiment revealed that having more forest and less development was beneficial. Though it is encouraging that there were no supported relationships that directly conflicted with each other, the inconsistency of the results at the territory scale may be an artifact of the different analyses used, or the fact that the principle components used to interpret the habitat variables were not exactly the same, thus not directly comparable. In the future, it would be useful to redo the analyses by running a PCA on *all* measured landcover so that the PCs were directly comparable. Also, box responses could be averaged over the three years of the correlational study and also analyzed using regression, so that the field experiment could be directly compared to the correlational study.

Table 16. A simplified comparison of predicted landcover relationships to the response variables (correlational analysis) to the results of the field experiment (n = 60 relocated boxes). Landcover variables describe which kind of habitat increases either occupancy or reproductive success.

SCALE	RESPONSE			
	Occupancy		**Reproductive Success**	
	Prediction	Experiment	Prediction	Experiment
Local	—	✔ *no relationships*	more grass, less forest	✔ *more grass*
Territory	more grass, less shrub	? *no relationships*	—	? *more forest, less development*

What do these findings mean for bluebirds on golf courses?

The results of this study help to explain why bluebirds have been a conservation success story. Their ability to use man-made nest boxes, and nest in a variety of edge habitats has made golf courses an important part of their population recovery. Though landcover around individual boxes have small and variable affects on occupancy and reproductive success, it seems to be that landcover at larger scales, such as the golf course and its surrounding landscape, may provide more information about where bluebirds are attracted, and how well they reproduce once they nest. More specifically, golf courses situated within highly developed areas will attract fewer bluebirds, but the most important feature is a golf course with lots of fragmented forest patches, as this explained up to 50% of the variation in reproductive success in our data. Within a golf course, placing boxes in areas with more grass can improve reproductive success. But since the bluebird population is doing well, it may be more important to place boxes in a variety of habitats on the golf course, so that other native cavity-nesting species, such as chickadees, titmice, and wrens, can take advantage of boxes that are less appealing to bluebirds. In addition, it helps to place predator guards on all nest boxes if possible.

What do these findings mean for other birds nesting on developed spaces?

A more accurate understanding of habitat effects can be obtained from studies addressing multiple years of data and multiple spatial scales of analysis, and care must be taken to choose scales that are biologically relevant the response of interest. This study successfully highlights the importance of these methodologies, and serves as a case study for other researchers interested in exploring the relationships between nesting habitat and avian life history traits. It also suggests that when carefully constructed and maintained, "greener" developed landscapes such as golf courses, farms, and parks could potentially be more useful for certain birds. With similar future studies, we may yet be able to share our world more responsibly with our avian neighbors.

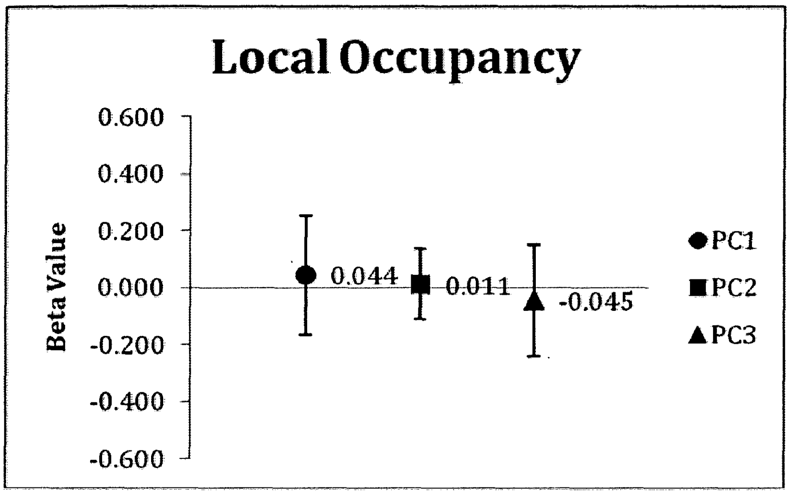
Appendix

Appendix A. Moran's I test results at the local and territory scales.

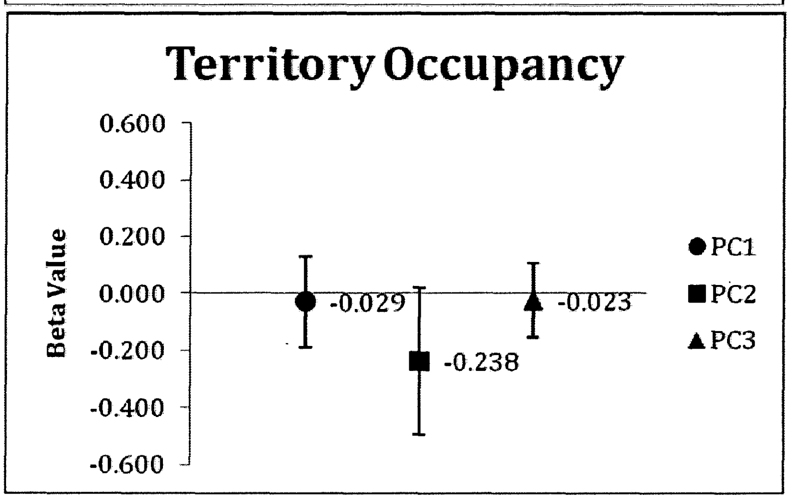
Scale	Golf Site	Data	PC1	PC2	PC3
Local	1	Moran's I	0.3	-0.03	0.02
		Z Score	1.98	-0.01	0.26
		Conclusion	somewhat clustered	random	random
	2	Moran's I	0.64	0.44	0.25
		Z Score	4.57	3.21	1.93
		Conclusion	clustered	clustered	somewhat clustered
	3	Moran's I	-0.05	0.06	0.17
		Z Score	-0.4	0.77	1.94
		Conclusion	random	random	somewhat clustered
	4	Moran's I	-0.1	-0.03	-0.06
		Z Score	-0.3	0.13	-0.02
		Conclusion	random	random	random
	5	Moran's I	0.13	-0.23	0.13
		Z Score	0.91	-0.98	0.83
		Conclusion	random	random	random
	6	Moran's I	-0.07	-0.05	-0.05
		Z Score	-0.54	-0.33	-0.35
		Conclusion	random	random	random
	7	Moran's I	-0.16	-0.01	0.39
		Z Score	-0.51	0.33	2.38
		Conclusion	random	random	somewhat clustered
	8	Moran's I	-0.04	-0.04	0.3
		Z Score	0.06	0.09	2.19
		Conclusion	random	random	somewhat clustered
	9	Moran's I	-0.05	-0.05	-0.05
		Z Score	-0.03	-0.02	-0.05
		Conclusion	random	random	random
Territory	1	Moran's I	0.22	-0.05	0.05
		Z Score	1.55	-0.12	0.5
		Conclusion	random	random	random
	2	Moran's I	-0.03	0.32	0.51
		Z Score	0.08	2.38	3.77
		Conclusion	random	somewhat clustered	clustered
	3	Moran's I	0.32	0.45	0.18
		Z Score	3.48	4.82	2.01

	Conclusion	clustered	clustered	somewhat clustered
4	Moran's I	0.06	0.05	0.42
	Z Score	0.72	0.67	3.01
	Conclusion	random	random	clustered
5	Moran's I	0.05	0.03	-0.08
	Z Score	0.46	0.34	-0.2
	Conclusion	random	random	random
6	Moran's I	0.33	0.38	0.3
	Z Score	3.48	4.02	3.48
	Conclusion	clustered	clustered	clustered
7	Moran's I	0.12	0.23	0.12
	Z Score	1.06	1.63	1
	Conclusion	random	random	random
8	Moran's I	0.23	0.1	0.48
	Z Score	1.62	0.87	3.21
	Conclusion	random	random	clustered
9	Moran's I	0.09	-0.25	0.08
	Z Score	0.81	-1.28	0.93
	Conclusion	random	somewhat orderly	random

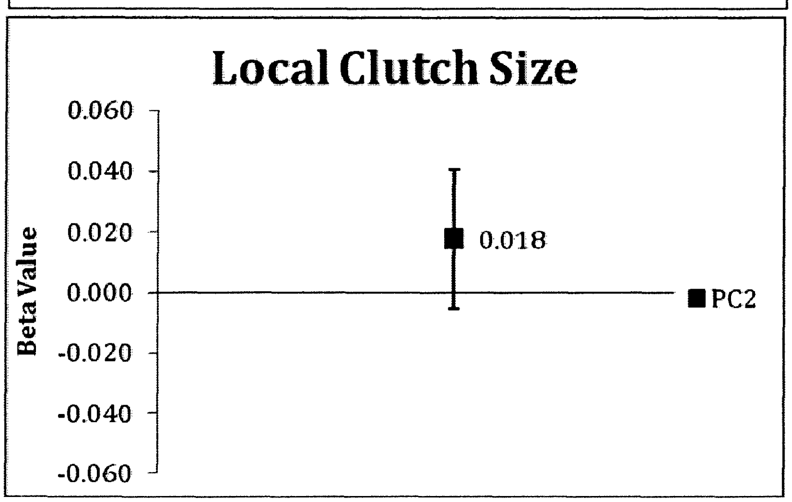
Appendix B. Landcover beta values and 95% confidence intervals of final models for each response variable at the local and territory scales: a,b = occupancy; c,d=clutch size; e,f=hatching success; g,h=fledging success.



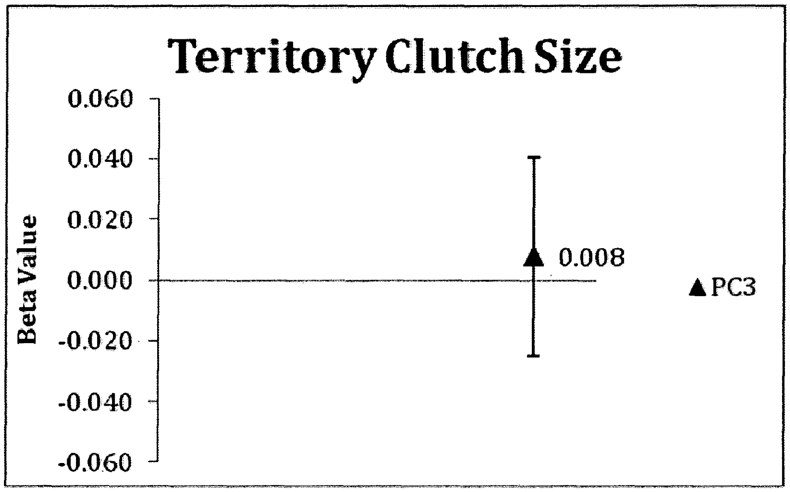
a)



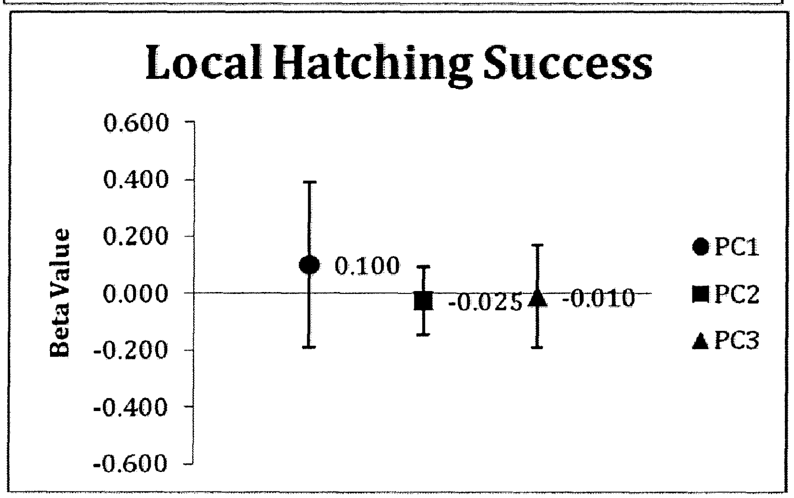
b)



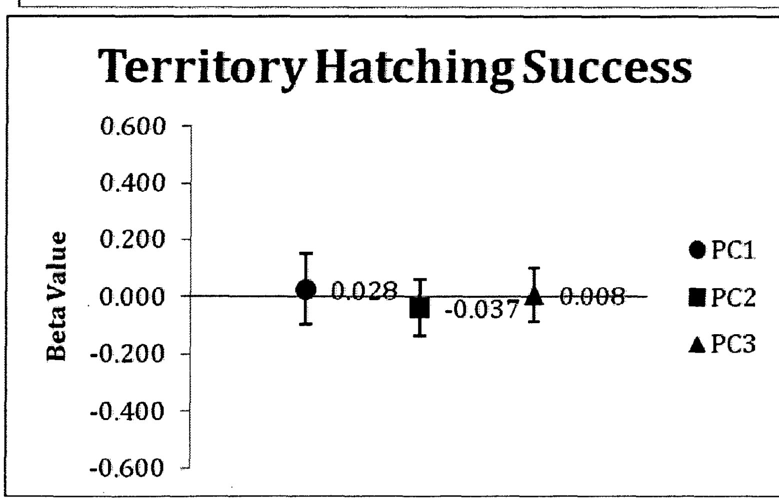
c)


Territory Clutch Size
0.060
0.040
0.020
0.000
-0.020
-0.040
-0.060
Beta Value
0.008
PC3

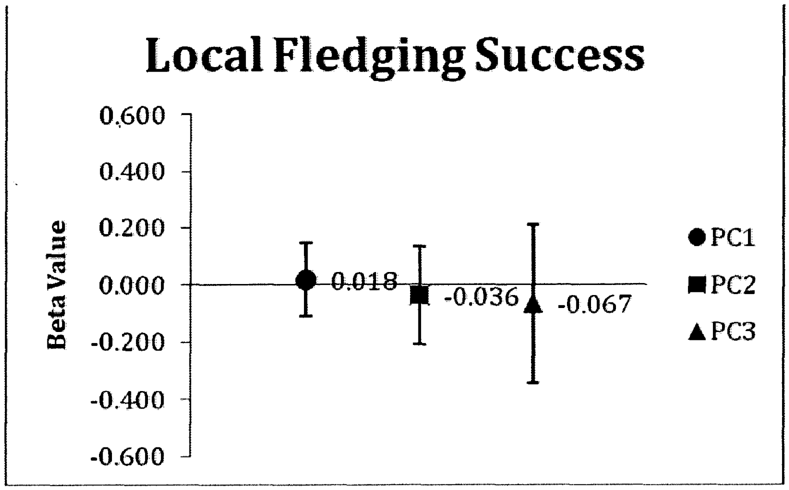
d)


Local Hatching Success
0.600
0.400
0.200
0.000
-0.200
-0.400
-0.600
Beta Value
0.100
-0.025
-0.010
PC1
PC2
PC3

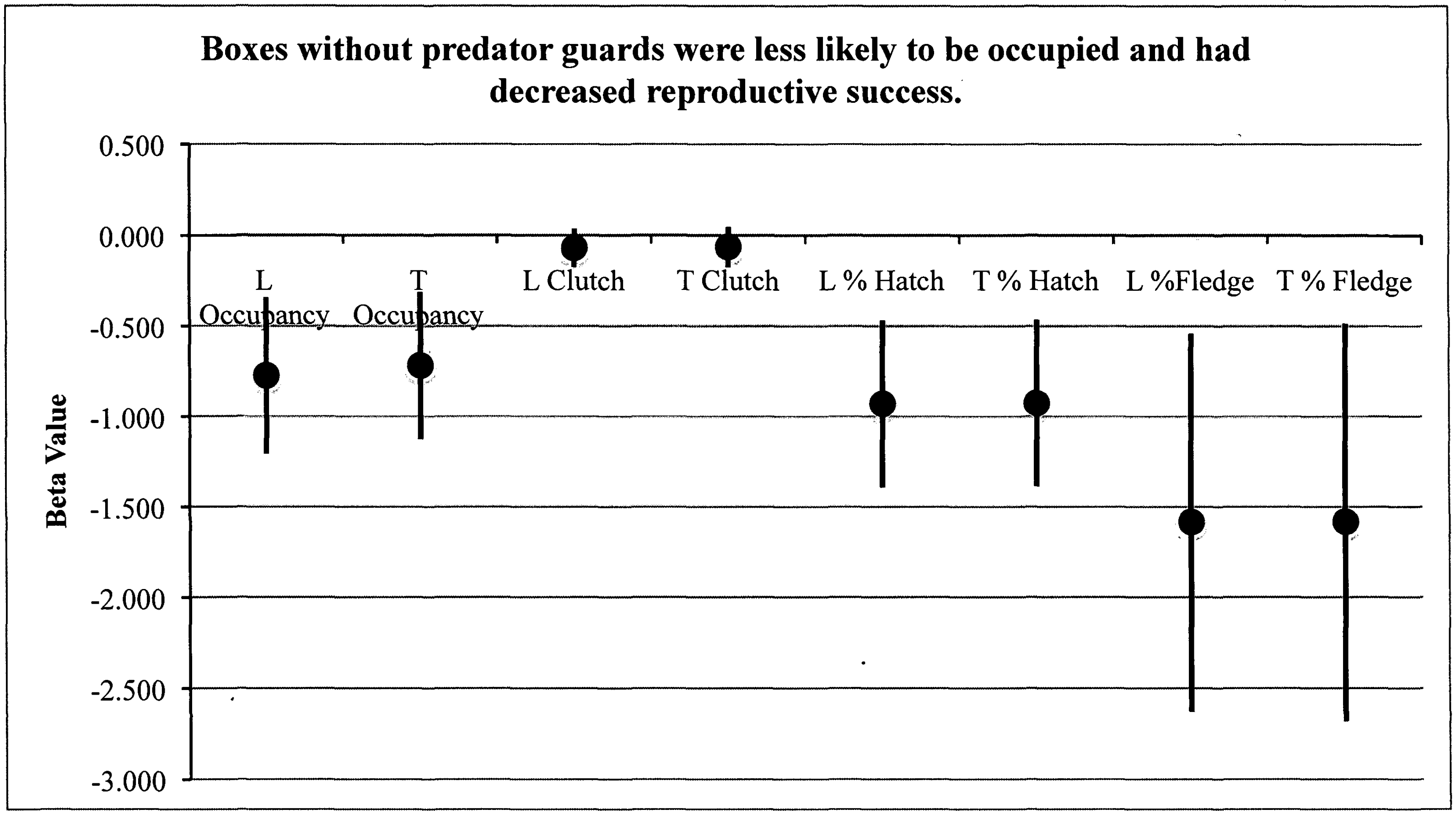
e)


Territory Hatching Success
0.600
0.400
0.200
0.000
-0.200
-0.400
-0.600
Beta Value
0.028
-0.037
0.008
PC1
PC2
PC3

f)

g) 
Local Fledging Success
0.600
0.400
0.200
0.000
-0.200
-0.400
-0.600
Beta Value
0.018
-0.036
-0.067
PC1
PC2
PC3

Appendix C. Beta values and 95% confidence intervals for the effect of *not* having a predator guard on response variables at the local (L) and territory (T) scales.



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LITERATURE CITED

Acevedo, M. A., and C. Restrepo. 2008. Land-cover and land-use change and its contribution to the large-scale organization of Puerto Rico's bird assemblages. Diversity and Distributions 14:114-122.

Betts, M. G. 2007. Thresholds in songbird occurrence in relation to landscape structure. Conservation Biology 21.

Bowers, M. A., and J. L. J. Dooley. 1999. A controlled, hierarchical study of habitat fragmentation: responses at the individual, patch, and landscape scale Landscape Ecology 14:381-389.

Breininger, D. R., V. L. Larson, B. W. Duncan, R. B. Smith, D. M. Oddy, and M. F. Goodchild. 1995. Landscape patterns of Florida Scrub Jay habitat use and demographic success. Conservation Biology 9:1442-1453.

Burnham, K. P., and D. E. Anderson. 2002. Model inference and multimodel selection. Academic Press, New York.

Colding, J., and C. Folke. 2009. The Role of Golf Courses in Biodiversity Conservation and Ecosystem Management. Ecosystems 12:191-206.

Cornell, K. L., and T. M. Donovan. 2009. Effects of spatial habitat heterogeneity on habitat selection and annual fecundity for a migratory forest songbird. Landscape Ecology 25:109-122.

Cristol, D. A., and A. D. Rodewald. 2005. Introduction: Can golf courses play a role in bird conservation? Wildlife Society Bulletin 33:407-410.

Dwernychuck, L. W., and D. A. Boag. 1972. Ducks nesting in associations with gulls: an ecological trap? Canadian Jounrnal of Zoology 50:559-563.

Environmental Research Institute, I. 2006. ArcGIS: Version 9.3. Redlands, California, USA.

Gange, A. C., D. E. Lindsay, and J. M. Schofield. 2003. The ecology of golf courses. Biologist 50:422-434.

Gordon, D. H., S. G. Jones, and G. M. Phillips. 2003. Golf Courses and Bird Communities in the South Atlantic Coastal Plain Turfgrass and Environmental Research Online 2:1-9.

Gordon, D. H., S. G. Jones and G. M. Phillips. 2004. Birds on golf courses in the South Atlantic coastal plain. Golf Course Management 72:95-99.

Gowaty, P. A., and J. H. Plissner. 1998. Eastern Bluebird (Sialia Sialis). in The Birds of North America. (A. Poole, and F. Gill, Eds.), Philadelphia, Pennsylvania.

Green, B. H., and I. C. Marshall. 1987. An assessment of the role of golf courses in Kent, England in protecting wildlife and landscapes. Landscape and Urban Planning 14:143-154.

Hodgkison, S. C., J. M. Hero, and J. Warnken. 2007. The conservation value of suburban golf courses in a rapidly urbanising region of Australia. Landscape and Urban Planning 79:323-337.

Hostetler, M., and K. Knowles-Yanez. 2003. Land use, scale, and bird distributions in the Phoenix metropolitan area. Landscape and Urban Planning 62:55-68.

Kight, C. R., and J. P. Swaddle. 2007. Associations of anthropogenic activity and disturbance with fitness metrics of eastern bluebirds (Sialia sialis). Biological Conservation 138:189-197.

Laurance, W. F. 2000. Do edge effects occur over large spatial scales? Trends in Ecology & Evolution 15:134-135.

LeClerc, J. E., J. P. K. Che, J. P. Swaddle, and D. A. Cristol. 2005. Reproductive success and developmental stability of eastern bluebirds on golf courses: evidence that golf courses can be productive. Wildlife Society Bulletin 33:483-493.

LeClerc, J. E., and D. A. Cristol. 2005. Are Golf Courses Providing Habitat for Birds of Conservation Concern in Virginia? Wildlife Society Bulletin 33:463-470.

Luck, G. W., and T. N. Korodaj. 2008. Stand and landscape-level factors related to bird assemblages in exotic pine plantations: Implications for forest management. Forest Ecology and Management 255:2688-2697.

Manly, B. F. J. 1990. Multivariate statistical methods. Chapman and Hall, New York, New York, USA.

McCarty, L. B. 2001. Best golf course management practices. Prentice Hall, Upper Saddle River, New Jersey, USA.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. . Pages Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html.

Merola-Zwartjes, M., and J. P. DeLong. 2005. Avian species assemblages on on New Mexico golf courses: surrogate riparian habitat for birds? Wildlife Society Bulletin 33:435-447.

Mitchell, B. R. 2008a. FragStatsBatch 9. [Online] Available at http://arcscripts.esri.com/details.asp?dbid=13995.

Mitchell, B. R. 2008b. Model Averaging Spreadsheet. [Online] Available at http://www.uvm.edu/~bmitchel/software.html.

National Golf Foundation. 2005. National Golf Foundation page summary statistics. www.ngf.org.

Pearce, F. 1892. How green is your golf? New Scientist 139:30-35.

Pennington, D. N., J. Hansel, and R. B. Blair. 2008. The conservation value of urban riparian areas for landbirds during spring migration: Land cover, scale, and vegetation effects. Biological Conservation 141:1235-1248.

Pleuramom, A. 1992. Course and effect: golf tourism in Thailand. Ecologist 22:104-110.

Porter, E. E., J. Bulluck, and R. B. Blair. 2005. Multiple spatial-scale assessment of the conservation value of golf courses for breeding birds southwestern Ohio. Wildlife Society Bulletin 33:494-506.

Ryder, T. 2010. Quantifying avian nest survival along an urbanization gradient using citizen- and scientist-generated data. Ecological Applications 20.

SAS. 2008. The SAS system for Windows. SAS Institute, Cary, North Carolina, USA.

SPSS, I. 1999. SPSS Base 10.0 for Windows User's Guide. SPSS Inc., Chicago IL.

Stanback, M. T., and M. L. Seifert. 2005. A comparison of eastern bluebird reproductive parameters in golf and rural habitats. Wildlife Society Bulletin 33:471-482.

Terman, M. R. 1997. Natural links: naturalistic golf courses as wildlife habitat. Landscape and Urban Planning 38:183-197.

Turner, M. G. 2005. Landscape ecology: What is the state of the science? Annual Review of Ecology Evolution and Systematics 36:319-344.

U. S. Geological Survey 2010. National Biological Information Infrastructure, Gap Analysis Program (GAP), National Land Cover, Version 1. [Online] Available at http://www.basic.ncsu.edu/segap/.

Venier, L. A., J. Pearce, J. E. McKee, D. W. McKenney, and G. J. Niemi. 2004. Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes Basin. Journal of Biogeography 31:315-331.

Weins, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Whithers, M. A., and V. Meentemeyer. 1999. Conepts of scale in landscape ecology. . Pages 205-252 in Mosaic Landscapes and Ecological Processes: Issues and Applications (J. M. Klopatek, and R. H. Gardner, Eds.). Springer-Verlag, New York.

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